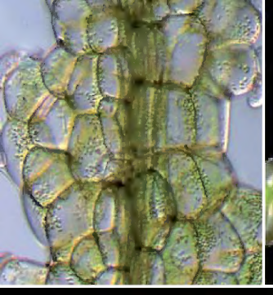
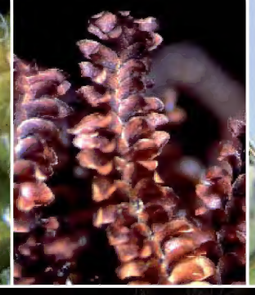




A Flora of the Liverworts and Hornworts of New Zealand

Volume 1

John J. Engel
David Glenny

A Flora of the Liverworts and Hornworts of New Zealand is an illustrated guide to an important component of New Zealand's green plant flora. The liverworts and hornworts, together with the mosses, make up the bryophytes. Liverworts are morphologically a more diverse group than the mosses in that they have both leafy and thallose forms, the leafy forms at times being mistaken for mosses. Volume 1 deals solely with leafy liverworts, as will Volume 2; Volume 3 will deal with the remainder of the leafy liverworts together with the thallose liverworts and the hornworts.

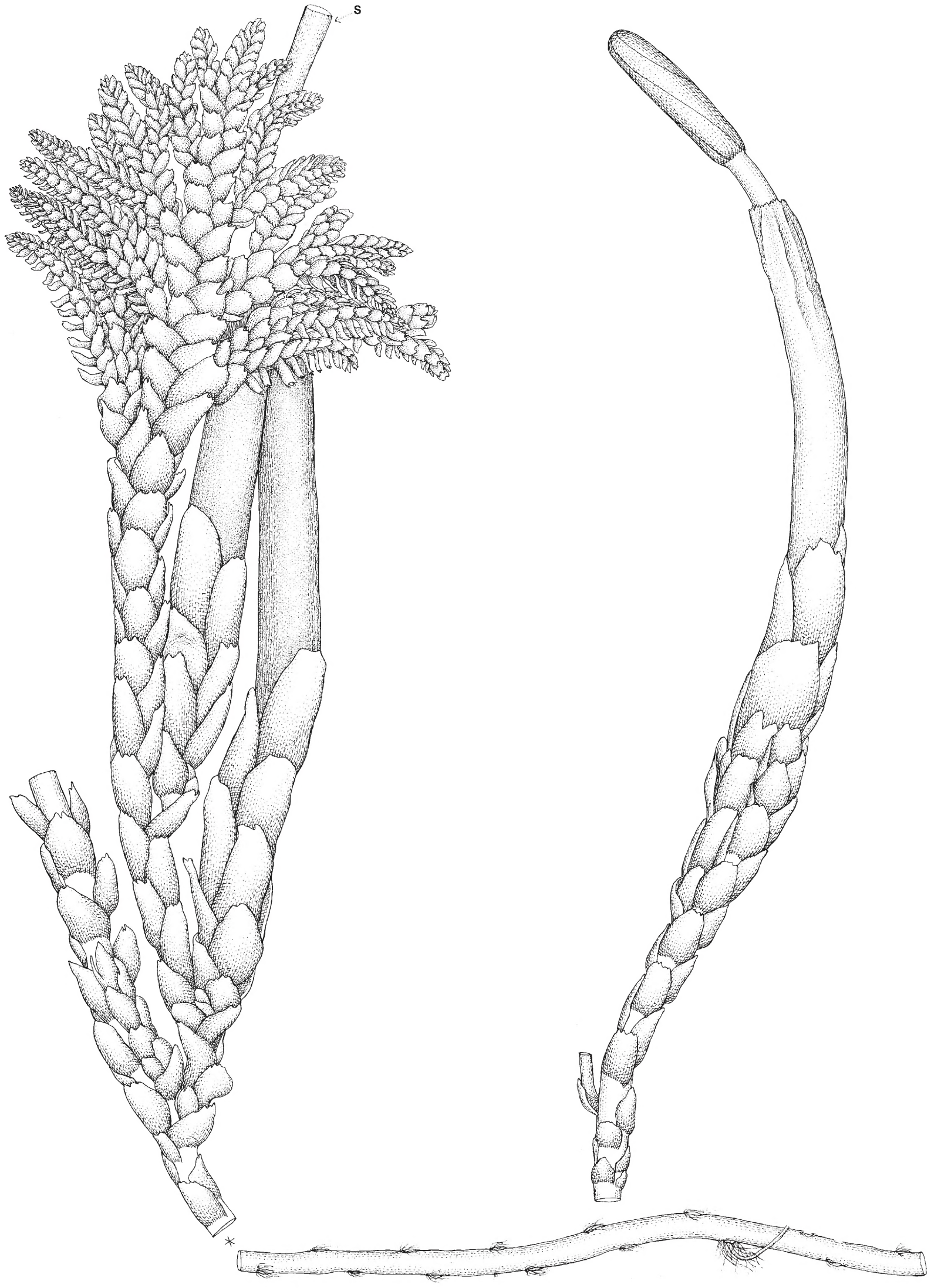
There are 595 species of liverworts and 13 hornwort species in 49 families and 157 genera that are currently accepted as occurring in the New Zealand region, defined here to include Kermadec, North, South, Stewart, and Chatham islands, as well as New Zealand's subantarctic islands — Auckland, Campbell, and Antipodes islands. This volume provides keys and descriptions to 211 of the 595 liverwort species, and provides a key to all genera of the largest order, the *Jungermanniales*. Detailed notes are provided on distribution and habitat, and discussions under the family and genus descriptions place the New Zealand flora in the context of the world liverwort and hornwort flora. To complement the descriptions, 172 black-and-white plates illustrate details of many of the species and 101 color images illustrate almost all of the 60 genera in this volume.

Volume 1 also includes a detailed Introduction, which presents a history of exploration of the New Zealand flora; provides a detailed overview of the region's climate, geology, and vegetation; and includes a special contribution on endophytic fungi associates in New Zealand liverworts and their ecological and evolutionary significance.

When this three-volume flora is completed, it will be the first flora for these two groups of bryophytes since Hooker's 1864–1867 *Handbook of the New Zealand Flora*.

A Flora of the Liverworts and Hornworts of New Zealand

Volume 1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A Flora of the Liverworts and Hornworts of New Zealand

Volume 1

John J. Engel
David Glenny

Missouri Botanical Garden
Landcare Research Manaaki Whenua
The Field Museum

A Flora of the Liverworts and Hornworts of New Zealand

Volume 1

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Table of Contents

INTRODUCTION 1
1. History of exploration and documentation of the flora 1
2. Biogeography of New Zealand's liverwort flora in the world context 13
3. Theories on origins of the present-day New Zealand liverwort flora 18
4. Ecological provinces of New Zealand 20
5. The climate of New Zealand 29
6. Geology and landforms of New Zealand 31
7. The vegetation of New Zealand 32
8. Principal substrates of New Zealand liverworts 36
9. Distribution and range of liverwort species within New Zealand 39
10. Rarity and conservation 41
11. Guidance to users of the flora 42
12. Endophytic fungi in New Zealand liverworts, by J. G. Duckett and R. Ligrone 48
13. Acknowledgments 56

Order 1. **CALOBRYALES** Campb. 59
Family **Haplomitriaceae** Dedecek 60
Haplomitrium Nees 60
Order 2. **JUNGERMANNIALES** H.Klinggr. 67
Suborder 1. **LEPICOLEINEAE** R.M.Schust. 93
Family **Lepicoleaceae** R.M.Schust. 94
Lepicolea Dumort. 95
Suborder 2. **NEOGROLLINEAE** J.J.Engel & Braggins 102
Family **Neogrolleaceae** (R.M.Schust.) J.J.Engel & Braggins 102
Neogrollea E.A.Hodgs. 102
Suborder 3. **HERBERTINEAE** R.M.Schust. 107
Family **Herbertaceae** Müll.Frib. 107
Herbertus Gray 108
Triandrophyllum Fulford & Hatcher 115
Family **Pseudolepicoleaceae** Fulford & J.Taylor 140
Isophyllaria E.A.Hodgs. & Allison 141
Temnoma Mitt. 147
Archeophylla R.M.Schust. 165
Family **Trichocoleaceae** Nakai 167
Castanoclobos J.J.Engel & Glenny 168
Leiomitra Lindb. 173
Trichocolea Dumort. 179
Eotrichocolea R.M.Schust. 191

Suborder 4. **LEPIDOZIINEAE** R.M.Schust. 194
Family **Lepidoziaceae** Limpr. 194
Subfam. ***Lepidozioideae***. 195
Lepidozia (Dumort.) Dumort. 195
Subg. ***Dendrolepidozia*** R.M.Schust. 201
Subg. ***Mastigolepidozia*** R.M.Schust. 204
Sect. ***Microphyllae*** (Lindenb.) Grolle 204
Subg. ***Notholepidozia*** R.M.Schust. 206
Sect. ***Pendulinae*** R.M.Schust. 206
Sect. ***Setigerae*** R.M.Schust. 209
Sect. ***Notholepidozia*** 211
Sect. ***Kirkii*** R.M.Schust. 248
Sect. ***Austrolepidozia*** R.M.Schust. 256
Subg. ***Glaucolepidozia*** R.M.Schust. 259
Telaranea Spruce *ex* Schiffn. 270
Subg. ***Acrolepidozia*** (R.M.Schust.) R.M.Schust. 276
Subg. ***Telaranea*** 279
Sect. ***Cancellatae*** J.J.Engel & Merrill 285
Sect. ***Ceraceae*** J.J.Engel & Merrill 309
Sect. ***Tricholepidozia*** (R.M.Schust.) J.J.Engel & Merrill 316
Sect. ***Transversae*** J.J.Engel & Merrill 324
Sect. ***Telaranea*** 339
Sect. ***Tenuifoliae*** (R.M.Schust.) J.J.Engel & Merrill 350
Kurzia G.Martens 358
Subg. ***Microlepidozia*** (Spruce) R.M.Schust. 361
Sect. ***Helophilae*** R.M.Schust. 361
Sect. ***Microlepidozia*** 364
Sect. ***Moniliformes*** J.J.Engel 373
Sect. ***Compactae*** R.M.Schust. 376
Subg. ***Dendrolembidium*** (Herzog) Grolle 379
Psiloclada Mitt. 381
Subfam. ***Drucelloideae*** (Boesen) R.M.Schust. 385
Drucella E.A.Hodgs. 385
Subfam. ***Bazzanioideae*** Rodway 390
Acromastigum A.Evans 390
Bazzania Gray 415
Sect. ***Protobazzania*** J.J.Engel 418
Sect. ***Connatae*** (Steph.) Fulford 423
Sect. ***Vittatae*** (Steph.) Fulford 442
Sect. ***Glaucobazzania*** J.J.Engel 449
Sect. ***Exemptae*** J.J.Engel 453
Subfam. ***Zoopsidoideae*** R.M.Schust. 457
Pseudocephalozia R.M.Schust. 457

Paracromastigum Fulford & J.Taylor 463
Hyalolepidozia S.W.Arnell *ex* Grolle 472
Zoopsis Hook.f. *ex* Gottsche, Lindenb. & Nees 477
Zoopsidella R.M.Schust. 495
Subfam. ***Lembidioideae*** R.M.Schust. 499
Isolembidium R.M.Schust. 499
Lembidium Mitt. 503
Hygrolembidium R.M.Schust. 509
Subg. ***Hygrobiellopsis*** R.M.Schust. *ex* Bedn.-Ochyra, Váňa, Ochyra & R.I.L.Sm. 511
Subg. ***Hygrolembidium*** 517
Chloranthelia R.M.Schust. 523
Subfam. ***Megalembidioideae*** J.J.Engel 525
Megalembidium R.M.Schust. 525
Family **Calypogeiaceae** Arnell 532
Calypogeia Raddi 533
Mnioloma Herzog 537
Suborder 5. **TRICHOTEMNOMATINEAE** J.J.Engel 542
Family **Trichotemnomaceae** R.M.Schust. 542
Trichotemnoma R.M.Schust. 543
Suborder 6. **ANTHELIINEAE** R.M.Schust. 546
Family **Antheliaceae** R.M.Schust. 546
Anthelia (Dumort.) Dumort. 547
Suborder 7. **CEPHALOZIINEAE** R.M.Schust. 551
Family **Cephaloziaceae** Mig. 551
Metahygrobiella R.M.Schust. 553
Cephalozia (Dumort.) Dumort. 559
Subg. ***Eocephalozia*** R.M.Schust. *ex* J.J.Engel 561
Subg. ***Cephalozia*** 565
Family **Cephaloziellaceae** Douin 566
Cephalomitrion R.M.Schust. 568
Allisoniella E.A.Hodgs. 570
Sect. ***Protomarsupella*** (R.M.Schust.) R.M.Schust. 572
Sect. ***Allisoniella*** 574
Cephaloziella (Spruce) Schiffn. 578
Subg. ***Schizophyllum*** Müll.Frib. 584
Subg. ***Cephaloziella*** 586
Subg. ***Evansia*** Müll.Frib. 604
Subg. ***Distichopsis*** R.M.Schust. 605
Family **Adelanthaceae** (Jörg.) Grolle 607
Pseudomarsupidium Herzog 609
Adelanthus Mitt. 615
Wettsteinia Schiffn. 628

Family **Jackiellaceae** R.M.Schust. 633
Jackiella Schiffn. 634
Suborder 8. **JUNGERMANNIINEAE** R.M.Schust. 637
Family **Jungermanniaceae** Rchb. 637
Subfam. ***Chandonanthoideae*** Inoue 640
Chandonanthus Mitt. 640
Subfam. ***Lophozioideae*** Macvicar 645
Lophozia (Dumort.) Dumort. 645
Subg. ***Protolophozia*** R.M.Schust. 648
Subg. ***Lophozia*** 662
Subg. ***Isopaches*** (Buch) R.M.Schust. 663
Tritomaria Schiffn. *ex* Loeske 666
Anastrophyllum (Spruce) Steph. 673
Andrewsianthus R.M.Schust. 685
Subg. ***Cephalolobus*** (R.M.Schust.) R.M.Schust. 688
Subg. ***Andrewsianthus*** 692
Subfam. ***Jungermannioideae*** 694
Solenostoma Mitt. 694
Subfam. ***Jamesonielloideae*** Inoue 713
Jamesoniella (Spruce) Carrington 713
Cuspidatula Steph. 726
Cryptochila R.M.Schust. 732
Family **Scapaniaceae** Mig. 744
Diplophyllum (Dumort.) Dumort. 746
Scapania (Dumort.) Dumort. 765
Sect. ***Scapania*** 768
Sect. ***Nemorosae*** (Müll.Frib.) Buch 769
Family **Blepharidophyllaceae** (R.M.Schust.) R.M.Schust. *ex* J.J.Engel 773
Clandarium (Grolle) R.M.Schust. 774
Blepharidophyllum Ångstr. 779
Family **Gymnomitriaceae** H.Klinggr. 783
Acrolophozia R.M.Schust. 785
Herzogobryum Grolle 788
Nothogymnomitrion R.M.Schust. 795
Marsupella Dumort. 798
Subg. ***Marsupella*** 799
Gymnomitrion Corda 805
APPENDIX: Species mentioned in this volume, including volume 2 and 3 liverworts 813
GLOSSARY 827
BIBLIOGRAPHY 845
INDEX 883

INTRODUCTION

1. History of exploration and documentation of the flora

First European visits to New Zealand

James Cook served as commander of three expeditions to the South Seas, with the first two most relevant to New Zealand botany. The first expedition (1768–1771) was commissioned to observe the 1769 transit of the planet Venus across the disc of the sun. Cook was commander of the *Endeavour*, and biological observations were the responsibility of Mr. Joseph Banks and Dr. Daniel Solander, a student of Linnaeus. The botanists collected plants at Poverty Bay (near the present city of Gisborne) and other localities on North Island, as well as Queen Charlotte Sound in the northern portion of the South Island (see comments in Cheeseman [1906, 1925] and Cockayne [1919]). Apparently no hepatics were published, but *Hymenophyton flabellatum* was collected and misidentified as a *Trichomanes* species (duplicate at WELT!). The second and greatest voyage of Cook (1772–1775) was on the vessels *Resolution* and *Adventure*, with John Reinhold Forster and his son, John George Adam Forster, serving as naturalists. The noted botanist Anders Sparrman, also a student of Linnaeus, joined the expedition in Cape Town. The observations made during this expedition "revolutionised knowledge of the southern hemisphere" (Godley, 1965, p. 146). New Zealand localities visited were Dusky Sound and Queen Charlotte Sound (see remarks in Cheeseman, 1906, 1925). Forster and Forster (1776) in their *Characteres Generum Plantarum* listed only one genus of cryptogams, *Aytonia*, based on *A. rupestris* (≡ *Plagiochasma rupestre*), but this was collected in the Madeira Islands (Schuster, 1992b). Of interest is the description of the new genus and species, *Monoclea forsteri* Hook. in Hooker (1818–1820). The protologue includes "Forster's MSS., Hab. Insulae australes. D. G. Forster (in Herb. Lambert.)." Given this information, the distribution of *Monoclea forsteri* and the route of the expedition, one of the Forsters probably collected the first New Zealand hepatic. Note here, incidentally, that Grolle and So (2003) concluded that the type specimen of *Jungermannia violacea* Ach. (≡ *Metzgeria violacea*), previously regarded as having been collected at Dusky Bay, New Zealand, on this expedition, actually was gathered in Tierra del Fuego on the same expedition (see also Hodgson, 1961). Cook's third and last voyage was with the *Resolution* and *Discovery* (1776–1780); William Anderson served as surgeon on the *Resolution* and made natural history collections. The expedition visited Queen Charlotte Sound, and although botanical collections were made at this site, liverworts apparently were not collected.

The Scottish surgeon-botanist Archibald Menzies (1754–1842) sailed on board H.M.S. *Discovery* as part of Vancouver's round-the-world voyage (1791–1795) and collected a number of liverworts as well as mosses and ferns at Dusky Sound during the period 2–22 November 1791 (for an account of this voyage see the volumes of Lamb, 1984). The liverwort collections, which are the first in New Zealand that are documented, were published in William Hooker's *Musci Exotici* (1818–1820). The *Musci Exotici* is noteworthy not only because of the introduction to science of such striking and conspicuous New Zealand hepatics as *Schistochila nobilis*, *S. appendiculata*, *S. glaucescens*, *Lepicolea scolopendra*, *Temnoma pulchellum* and several others, but also because of the handsome, accurate colored plates that remain useful nearly two centuries later. He is commemorated by *Jungermannia menziesii* Hook. (≡ *Lepidogyna menziesii*) of southern South America. Menzies published little himself, but the impact of his

hepatic collections is highly significant. For information on his botanical activities in New Zealand see Godley (1960), Galloway (1985, 1991, 1995) and Galloway and Groves (1987).

French, American and British natural history expeditions of the early nineteenth century

During his first voyage to the Pacific (1822–1825), Jules Sébastien César Dumont d'Urville (1790–1842) visited New Zealand on board the *Coquille* under the command of L. I. Duperrey. Lieutenant d'Urville, an ardent botanical collector, was assisted by René Primivère Lesson, who served as naval doctor and naturalist. The expedition remained at Bay of Islands for nearly two weeks. The second voyage to the Pacific by Dumont d'Urville was aboard the same vessel, which was renamed the *Astrolabe* (1827–1829), under his command, and Pierre Adolphe Lesson, brother of René, accompanied the voyage as botanist. In New Zealand botanical collections were made at Tasman Bay and the "French Pass," which separates d'Urville Island and the mainland, and Tolaga Bay and Auckland Harbour on North Island. Achille Richard (1832) published a botanical account of this expedition and included the species collected on the earlier d'Urville expedition as well as most of the collections made by Forster on Cook's second voyage (Cheeseman, 1906, 1925). However, the account of the Hepaticae in Richard (1832) included enumeration of 28 species, and of these, all except four were cited as having been collected by Menzies. No collector is cited for the remaining four species; whether they were collected on either the first or second expedition of d'Urville, or by the Forsters, remains unknown. d'Urville's third voyage to the Pacific is the most important for our purposes and involved two corvettes, the *Astrolabe* and the *Zélée*, during the years 1837–1840. d'Urville served as commander of the *Astrolabe*, and botanical collecting was the charge of Jacques Hombron, the senior surgeon on the *Astrolabe*. The *Zélée* was commanded by Charles Jacquinot; Honoré Jacquinot served as junior surgeon on this ship and was responsible for the collection of plants. The expedition visited New Zealand and (12–20 March 1840) Auckland Island, the latter botanized for the first time. The hepatics were studied by Camille Montagne, who published a preliminary account (Montagne, 1843) that included the introductions of *Jungermannia schismoides* Mont. (≡ *Anastrophyllum schismoides*) and *Madotheca elegantula* Mont. (≡ *Porella elegantula*), both described from the Auckland Islands. The full account appeared in Montagne (1845a) and, together with Montagne (1843), included a number of types based primarily on the collections of Hombron and Jacquinot.

The second United States Exploring Expedition (1838–1842) was prompted by a desire to obtain information on the South Pacific, an area that was rapidly becoming of interest to American traders and whalers. Commanded by Lieutenant Charles Wilkes of the United States Navy, it included a contingent of scientists among whom was botanist William Rich (1800–1864); for further comments see Godley (1965). The expedition briefly visited New Zealand and also Auckland Island in 1840. Any hepatics collected in New Zealand were apparently unpublished; Sullivant (1850) published on the hepatics collected at Orange Harbour, Tierra del Fuego.

Of the expeditions to Austral areas during this time period, the most important was that of the British voyages of *Erebus* and *Terror* (1839–1843). The period of this exploration is also notable, since it coincides with the beginnings of systematic colonization of New Zealand by Europeans in 1840. Botanists on the expedition were Joseph Dalton Hooker (1817–1911, son of William Jackson Hooker), who served as assistant surgeon on the *Erebus* (James Clark Ross was captain), and David Lyall, assistant surgeon on the *Terror* (under F. R. M. Crozier, com-

mander). Hooker made the first extensive collection of plants from Auckland Island on 20 November–12 December 1840 (Hombron having collected there earlier that year) and was the first to make botanical collections on Campbell Island, which he visited during the period of 13–17 December 1840 (Godley, 1965). The vessels spent the period of 18 August–17 November 1841 at the Bay of Islands, and during the period Hooker actively collected plants, often in the company of William Colenso and Dr. Andrew Sinclair (see below). Many of the liverwort collections from Auckland and Campbell Islands and New Zealand are types.

In the autumn of 1843 Hooker invited Thomas Taylor (1786–1848; cf. Sayre, 1983, 1987) to examine some or all of the cryptogams that were collected as part of the expedition. Taylor replied (Sayre, 1987, p. 423), "'I should be very proud to be associated once again in any scientific exertion with the name of Hooker; I will therefore most cheerfully undertake to examine, and if you please it, give specific characters and short descriptions of any Cryptogamic plants you may commit to me' (TT to JH, 20 November 1843, K)." Taylor received the first specimens from Hooker in November 1843. Sayre (1987, p. 423) provided valuable insights in the way of Taylor's involvement with the hepatic publications. "The first question was whether Taylor should use the new generic names proposed by Nees von Esenbeck. 'While it would be desirable to keep pace with modern improvements on the one hand, on the other, the improvements are questionable, the generic characters being scarcely sufficient or strictly drawn from the parts necessary to fructification. In other words, the difficulty of subdividing *Jungermannia*, with few exceptions, remains as great as it was 30 years ago' (TT to JH, 20 November 1843, K). Taylor recommended that all leafy liverworts should be called *Jungermannia*, but arranged in sections headed with Nees's generic names. This system was followed in the series of four papers published in 1844 and (the Supplement) 1845 to secure the priority of the new names, and in Hooker's *Botany of the Antarctic Voyage* in 1845 and 1847.

"He also had to take account of Montagne's Plantes cellulaires in Dumont d'Urville's *Voyage au Pôle sud* (published in parts in 1843 and 1844). Hooker had copied out the appropriate parts of Montagne for Taylor. Taylor had sent many Antarctic hepatics to Montagne and received in return seven of the thirteen species that had already been published. Taylor wrote to Hooker, 'I am delighted that we shall, so far, be spared the shame of publishing as new what Montagne had already given.... This is a noble Frenchman!' (TT to JH, 7 August 1844, K)."

The hepatic collections from Auckland and Campbell Islands and New Zealand were worked up by Thomas Taylor, and details first appeared in the *London Journal of Botany* (Hooker and Taylor, 1844a, 1844b, 1845). It is notable to call attention again here that Taylor received the first specimens from Hooker in November 1843, and, by 1 February 1845 the above-mentioned three papers were published in the *Journal* (see Bibliography). Taylor alone, or, more often, with J. D. Hooker, published as new 183 of the 260 taxa included in the two articles and the supplement (comprising Hooker and Taylor, 1844a, 1844b, 1845 [Sayre, 1983]). A few additions to the New Zealand flora appeared in Taylor (1846); these are attributed to "Hook. f. & Tayl." In Hooker and Taylor (1845) specimens of Cunningham and some from the herbarium of Robert Greville were added to those of Hooker. Hooker's involvement and perspective may be found in the preface to his account of hepatics in the Handbook (Hooker, 1864–1867, p. 498), where he remarked that the hepatics "were placed, at the late Dr. Taylor's request, in his [Taylor's] hands for immediate publication, and the descriptions of many appeared, in 1844, in Hooker's 'London Journal of Botany,' and again in the 'Botany of the Antarctic Voyage.' At that time the valuable 'Synopsis Hepaticarum' of Gottsche, Lindenberg and Nees von Esenbeck was not published (it was not completed till 1847), and the difficulty of ascertaining and defining species was very great indeed. Owing to this cause and to Dr. Taylor's precipitancy in publication, much confusion crept into his work; the same plant

appearing under several generic names, and some descriptions answering to subsequently cancelled species, having been also published as good species." Hooker continued but, qualifying his comments somewhat, remarked (p. 499) that "whilst feeling it is my duty to make these facts clearly known, I must add, that those who study this extensive Order of plants by the aid of modern works, can have no conception of the difficulties which Dr. Taylor had to overcome, twenty-two years ago, in classifying and naming 300 or 400 *Hepaticae* with which I supplied him, and of which not fifty had been published; imperfect and hasty as his work was, it showed great skill, no little sagacity, and indomitable perseverance as a microscopic investigator."

The papers published in the *Journal* appeared prior to publication of the liverwort sections in the *Flora Antarctica*—the portion covering Auckland and Campbell Islands appeared in Taylor and Hooker (1845), which appeared on 1 May 1845, a few months after publication of Hooker and Taylor (1845), which appeared on 1 February. Sayre (1983, p. 467) provided insight into the role of Hooker in joint publication with Taylor, with Hooker stating that "'after a thorough examination by Dr Taylor, the specimens have twice passed under my own eyes, preparatory to the completion of the descriptions and the drawings' (JH's footnote, p. 114). Actually, the descriptions were completely rewritten from their first form in the *Journal of Botany*. Taylor commented: 'I hardly recognized the brats in their Sunday clothes' (to JH, 20 April 1845, K). A number of species had been added, included 16 new, but almost all the new taxa of the *Journal* paper have been retained." Taylor died before the publication of the *Flora Novae-Zelandiae* volume, and William Mitten (1819–1906) prepared the hepatics for the volume covering New Zealand (Mitten, 1854–1855) and Tasmania (Mitten, 1854–1855). Some of the species enumerated in the *Flora Antarctica* are illustrated with hand-colored illustrations.

Little information relevant to the specific localities of liverwort collections made on the *Erebus* and *Terror* expedition may be obtained from the publications of the hepatics in the *London Journal of Botany* or in the *Flora Antarctica* (see below). For example, the only specific locality cited for the 37 Hooker species enumerated in the Hepaticae section published in Hooker's *Flora Novae-Zelandiae* (Mitten, 1854–1855) is Bay of Islands.

Collectors in the early New Zealand British colony

The *Flora Antarctica* included not only the specimens of Joseph Hooker, but also a number of collections that were sent to Kew by various New Zealand correspondents of Joseph Hooker and his father, William Hooker (see Galloway, 1998, 2004). These citations provide insight into the identity of the collectors and the localities visited by those individuals who were engaged in botanical pursuits that included the collection of liverworts in the early New Zealand colony. The collectors are:

Lieutenant-Colonel Daniel Bolton—6 species cited, all from Auckland. Bolton collected on the Auckland Islands in 1850 (Godley, 1970, p. 49; 2003); all "Auckland" records in Mitten (1874–1855) are from the vicinity of Auckland city.

William Colenso—collections of 129 species cited, all from North Island (see below).

Allan Cunningham—5 species cited, all from Bay of Islands where a specific locality is mentioned. It should be noted that Allan Cunningham (1791–1839), Government Botanist and Superintendent of the Sydney Botanical Gardens, traveled to New Zealand in 1826 and spent over five months collecting. His brother, Richard Cunningham (1793–1835), trav-

eled to New Zealand in 1833. Both collected in the Bay of Islands, Whangaroa and Hokianga districts.

John Edgerley—1 species from the North Island.

John Jolliffe—5 species cited, 4 from Hokianga, 1 cited only as North Island.

Dr. David Lyall—60 species, with the following localities mentioned: Auckland and Port Nicholson in the North Island; Port Cooper, Canterbury Plains, Chalky Bay [Chalky Inlet], Port Preservation, Thomson's Sound, Bligh's Sound and Milford Sound in the South Island; and Port William on Stewart Island. David Lyall (1817–1895) served as surgeon-naturalist on the *Acheron*, under the command of Captain Stokes, which surveyed the coast of New Zealand, particularly the western and southwestern sectors, in 1847–1851; Lyall gave particular attention to lower plants. Localities visited during that expedition included Milford Sound, Chalky Inlet, Dusky Bay, Preservation Inlet and both shores of Foveaux Strait. He is commemorated by *Isotachis lyallii* Mitt.

Archibald Menzies—31 species from Dusky Bay made during the Vancouver expedition (see above).

Etienne Raoul—3 species cited, all from Akaroa, Banks Peninsula, South Island (see below).

William Rich—1 collection from a "small island off Auckland" (Mitten, 1854–1855, p. 127); see above under United States Exploring Expedition.

Dr. Andrew Sinclair—34 species cited, all from North Island, including Auckland, Bay of Islands, East Cape, Waikehi and Mt. Egmont (Mt. Taranaki). Sinclair (1794–1861) was colonial secretary of the British administration of New Zealand in 1844–1856 and actively pursued plant collecting, particularly in retirement; he drowned in an attempt to ford the Rangitata River on an expedition. Sinclair initially collected in the North Island, and later in Nelson as well as inland Canterbury, where he participated in botanical and geological surveys. Joseph Hooker considered Sinclair second only to Colenso as a botanical explorer (Cockayne, 1919, p. 10); Sinclair sent his materials to Kew.

Sowerby—1 species with no specific locality provided.

W. Stephenson (?1810–ca. 1863)—23 species cited; most have a specific locality and all of these are from the Wellington area.

Hooker played an important role in the development of New Zealand botany during these years "for he provided a direct and personal link between the few isolated plant collectors in New Zealand, and the wider botanical and scientific world of which the Royal Botanic Gardens at Kew was such a centre and focus" (Galloway, 1998, p. 35).

Volume one of Hooker's *Flora Novae-Zelandiae*, containing the flowering plants, appeared in 1853, and the second volume, covering the cryptogams, appeared in 1854 and 1855. The decade that followed saw considerable botanical activity in the New Zealand colony. The period also had rapid settlement of the South Island, which was followed by exploration and botanical investigations of that island. A need for a concise account of the flora of the colony emerged, and Charles Knight (see below), a long-time correspondent with Hooker, obtained a government commission for Joseph Hooker to prepare such a publication. Hooker published the *Handbook of the New Zealand Flora* in two parts; the flowering plants and ferns appeared in 1864 and the concluding part, containing Hepaticae, mosses, lichens, fungi and algae, appeared in 1867. Hooker initially intended the Handbook to cover only the flowering plants, and in preparation of the second part, he relied on several cryptogamists for preparation of specific groups. Hooker (1864–1867), in the preface of the hepatic account, remarked (p. 499) that "In the present work I have followed in Mr. Mitten's footsteps, he having drawn up all the

descriptions for the 'Flora Novae-Zelandiae,' with great care; and to him, too, I am indebted for naming the species of this Order received since the publication of that work; he has also detected many of Dr. Taylor's errors, and rediscovered, in later collections, many of his lost species." The treatment of liverworts was the first and one of only two accounts that provided a more comprehensive treatment of the hepatics of New Zealand. The publication of the Handbook is an important milestone in New Zealand botany, and in this connection Galloway (1998, p. 31) remarked that "for a small colonial government to commission one of the scientific world's most illustrious botanists to devote at least three years of his life to such a task was no mean achievement." Moreover, the Handbook "put New Zealand botany on the map, both nationally and internationally, in a manner that was accessible and interesting to a wide audience who were clamorous for information on the natural history of the colonies" (Galloway, 1998, p. 32).

During a similar time frame that Hooker visited New Zealand, Etienne Fiacre Louis Raoul (1815–1852) served as surgeon on the French corvette *L'Aube* (later replaced by *L'Allier*) and was stationed at Akaroa on the Banks Peninsula (1840–1843). Raoul was the first botanist to collect on the eastern side of the South Island and sent a complete set of specimens to Kew where they were made available to Thomas Taylor. As a result, Raoul's new finds from Akaroa were published by Hooker and Taylor or Hooker and Levier, and listed in the *Choix de Plantes de la Nouvelle Zélande* (Raoul, 1846). This publication included a list of New Zealand plant species known to that date, including 10 liverwort and one hornwort species (Macmillan, 1998).

Mid-nineteenth-century synoptic work

During the mid-nineteenth century several major synoptic works appeared. Johann Georg Christian Lehmann (1792–1860; *Jungermannia lehmanniana* Lindenb. ≡ *Schistochila lehmanniana*) published his *Novarum et Minus Cognitarum Stirpium Pugillus* series (1828–1857), and five species from New Zealand were described as new, four based on Menzies collections from Dusky Bay (*Anthoceros denticulatus*, *A. giganteus*, *Jungermannia anisostoma*, *J. novaezeelandiae* and *J. praenitens*). Gottsche, Lindenberg and Nees (1844–1847) published a compilation of the hepatics known to that date in their *Synopsis Hepaticarum* and included numerous references to New Zealand hepatics, many in newly introduced genera that segregated a number of species from the large portmanteau genus *Jungermannia* (see above comment on Taylor, who worked during the same period).

A German expedition to observe the transit of Venus visited the Auckland Islands, arriving on the *Alexandrine* on 15 October 1874 and remaining until 6 March 1875 (Godley, 1965). Hepatics were collected by Hermann Krone, who served as photographer on the expedition; at least some of Krone's hepatic collections were studied by Stephani.

New Zealand–based collectors and botanists of the late nineteenth century

During the late nineteenth century several advancements were made relevant to New Zealand liverworts. Foremost among contributors is the Reverend William Colenso, who "was the last, and the greatest, of the missionary explorers" (Temple, 1985, p. 11). Colenso traveled nearly the whole of the North Island, all on foot, and was the first European to penetrate inland to any appreciable extent. For example, he was the first European to reach Lake Waikaremoana and

the first to cross the Ruahine Range. Colenso published 59 botanical papers in the *Transactions of the New Zealand Institute*, of which 13 included hepatics. His papers that included liverworts spanned the years 1881 to 1893 and contained 217 new species. All but about 25 of these names are synonyms, but Cheeseman (1906, p. xxv; 1925, p. xxvi) provided an interesting perspective, "that [this] is a circumstance which must not detract from the recognition of his undoubted services to the botany of New Zealand." A complete list of Colenso's papers that included hepatics are included in the Bibliography section of this volume; for his collections held at WELT see Hamlin (1971). Stephani (1892) described a number of new species collected by Colenso and provided a disposition of the species described by Colenso. Colenso is commemorated by several liverwort names, among them *Schistochila colensoana* Steph. (≡ *Pachyschistochila colensoana*), *Mastigobryum colensoanum* Mitt. (≡ *Acromastigum colensoanum*) and *Lopholejeunea colensoi* Steph. A few other individuals were cited in Colenso's works as having gathered liverworts, among them Augustus Hamilton (1854–1913), director of the Colonial Museum in Wellington between 1903 and 1913 who collected Hepaticae at Okarito and the Hawke's Bay District in the foothills of the Ruahine Range and places on the eastern side of North Island. Mr. Henry Hill (1849–1933), school inspector and mayor of Napier, collected in Hawke's Bay, Gisborne, Urewera, Ruahine Range and Tongariro National Park between 1885 and 1898 and sent his specimens to Colenso.

Charles Knight (1808–1891), the New Zealand Government Auditor-General, published a series of papers on lichens, his main botanical interest, and a few on mosses during the period of 1860–1884 (Galloway, 1990, 1998). Knight also collected liverworts and is commemorated by several names, among them *Marsupidium knightii* Mitt. and *Chiloscyphus knightii* Steph. (≡ *Heteroscyphus knightii*).

Dr. Lauder Lindsay (1829–1880), a British physician, collected in eastern Otago in 1861–1862. Data on liverworts were published in Lindsay (1867), and a list of 10 species of hepatics and one anthocerote appeared in Lindsay (1868), which presently is a notably rare publication.

Thomas Kirk (1828–1898; cf. MacLeod, 1993; Moore, 1973) arrived in New Zealand in 1863, residing for 10 years in Auckland before moving to Wellington, and for many years "held the position of leader of botanical thought in New Zealand" (Cockayne, 1919, p. 11). Kirk published many papers (nearly 150, mostly in the *Transactions of the New Zealand Institute*), chiefly on flowering plants, during the period of 1869 to 1899 (for a list see Allan, 1982). These included "The Forest Flora of New Zealand" (Kirk, 1889), a major contribution. His botanical excursions included both North Island and South Island. In 1890 Kirk visited several islands on board the *Hinemoa*: Auckland Islands (10–12 January 1890), Campbell Island (13–14 January 1890), Snares Islands and Antipodes Islands. During his botanical excursions Kirk collected a number of liverworts, many of which were sent to Stephani for study. Kirk's collections from Great Barrier Island are particularly noteworthy. Kirk is commemorated by the following Stephani species: *Frullania kirkii* (≡ *Frullania patula*), *Jamesoniella kirkii, Lepidozia kirkii*, *Cephalozia kirkii* (= *Paracromastigum macrostipum*) and *Schistochila kirkiana* Steph.

Other New Zealand botanists with a primary interest in flowering plants also collected liverworts. Among them was Thomas Frederick Cheeseman (1845–1923; cf. Cockayne, 1923), botanist, author of *Manual of the New Zealand Flora* (Cheeseman, 1906, 1925), director of the Auckland Institute and Museum for 50 years, and author of over 240 angiosperm names (Ewen Cameron, *in litt.*); he was commemorated by *Lophocolea cheesemanii* Steph. (= *Chiloscyphus lentus*). Others are Donald Petrie (1846–1925), who resided in Otago for over 20 years and was Chief Inspector of Schools for Otago and later held the same position in Auck-

land. While in Otago he traveled to the eastern, central and southern portions of Otago Province and was the first to provide a description of the flora and vegetation of Stewart Island. Leonard Cockayne (1855–1934; cf. Laing, 1936) published works during the period 1899–1934 and made important contributions to higher plants, including *The Vegetation of New Zealand* (Cockayne, 1921) and the popular work *New Zealand Plants and Their Story* (Cockayne, 1919). He collected liverworts on Stewart Island in 1908 for the Department of Lands and Survey (Cockayne, 1909a), and his collections were studied by Stephani. Cockayne is commemorated by *Calycularia cockaynei* Steph. (≡ *Allisonia cockaynei*). Henry H. Travers (1844–1928) of Nelson visited the Chatham Islands twice, in 1864 to collect for Ferdinand von Mueller of Melbourne, and in 1870. Travers made a living as a collector of natural history material, selling live and pressed plants to horticulturists and museums in New Zealand and overseas. Some of his hepatic collections were cited by Stephani in his *Species Hepaticarum* (Lyon et al., 1971, p. 704).

John Buchanan (1819–1898; cf. Adams, 2002), naturalist and draughtsman, published a number of papers, mainly on flowering plants, during the period of 1870 to 1885 (for a list see Allan, 1982). Buchanan collected on mainland New Zealand and also sailed aboard the *Stella*, a New Zealand Government steamer, to Campbell and Auckland Islands in 1883. There remains some uncertainty as to the whereabouts of Buchanan's collections. Adams (2002, p. 109) remarked that "until a search is undertaken, especially in the collections of Glasgow and Edinburgh, our knowledge must remain as fragmentary as the known Buchanan specimens that have survived in New Zealand, mainly in the herbarium of the Colonial Museum (Te Papa) and the Otago Museum. The latter collection has been deposited by the Trustees of the Otago Museum in the herbarium of Te Papa (WELT)." Some Buchanan collections came to Te Papa from the Otago Museum, as mentioned by Adams (2002). Lyon et al. (1971) noted that some bryophyte collections are at the University of Otago (OTA) on indefinite loan from the Otago Museum, that these are in good order, that some were named by J. D. Hooker and that the unnamed specimens were revised by K. W. Allison. John Steel (*in litt.*) is of the opinion that the specimens were transferred to the University of Otago in the early 1960s. Barry Sneddon of the herbarium at Te Papa commented (*in litt.*) that "there is a Buchanan guard book bearing the label 'N.Z. Hepaticae' on the front cover. This book contains approximately 85 pages of which ca. 63 have 1–4 liverwort species per page and the rest of the pages have no specimens. In spite of its title, the book does contain a few foreign liverworts (all[?] from Britain), but the great majority are from New Zealand. There is a wide range of genera represented, but the accompanying information is restricted to genus and species and (not always) locality (Otago & Wellington). There are no dates. Below one specimen Buchanan has written '*Plagiochila subsimilis* n.s. Colenso' as the only information. Te Papa also holds 3 boxes of his specimens labelled 'Buchanan – Miscellaneous.' ... One box has a folder on which someone (Nancy Adams, perhaps) has pencilled: 'J. Buchanan ex O.M. / Bryophytes mounted/named no locality, in "Otago Witness" [a Newspaper] of Sep. 2 1887.' This folder contains a mixture of liverworts and (preponderantly) mosses."

Franz Stephani (1842–1927; cf. Beauverd, 1927; Geissler, 1982) played a significant role in the advance and development of New Zealand hepaticology, since for a number of years many individuals in varied circumstances sent him New Zealand material. This resulted in many names described by him. Many of the new species appeared in *Hedwigia*, e.g., *Blepharostoma corrugatum* Steph. (≡ *Trichotemnoma corrugatum*), and a great number were published in "Species Hepaticarum" (1898–1924).

Richard Helms (1842–1914; cf. Godley, 2001) was a self-taught naturalist of Greymouth who sent moss and liverwort specimens from the Paparoa Range and the vicinity of Grey-

mouth to Cosmo Melville in England. These were forwarded to Henry Boswell and were later seen by Müller, who published a number of new mosses from this material, and by Stephani, who described *Anthoceros helmsii*, *Lejeunea helmsii* and *Lophocolea helmsiana* (≡ *Chiloscyphus helmsianus*) from Helms's collections.

T. W. N. Beckett (1839–1906) was an orchardist who immigrated to Christchurch in 1883 and who collected liverworts mainly on the Christchurch to Greymouth rail route, but also on Banks Peninsula, North and South Canterbury foothills, Hawke's Bay and Kaikoura during the period of 1883–1904 (Godley, 1967; Lyon et al., 1971). Beckett was an important collector of mosses; his private herbarium, which is now housed at CHR, contains 15,000 moss specimens, and he exchanged material with leading overseas muscologists such as Brotherus (Fife, 1985). He sent liverwort specimens to Stephani and Levier. Five hundred hepatic specimens are in Beckett's herbarium at CHR, and while most specimens are Beckett's, there are also duplicates of collections made by Buchanan, Cheeseman, Cox, Hill, Kirk, Petrie and Rutland. Stephani named two species after Beckett, *Mastigophora beckettiana* Steph. (= *Triandrophyllum subtrifidum*) and *Lepidozia beckettiana* Steph. (= *Telaranea praenitens*).

European collectors in the late nineteenth century

Max Fleischer (1861–1930) collected liverworts in New Zealand in 1903 during his return to Germany from Java, where he gathered mosses for his *Die Musci der Flora von Buitenzorg* (Fleischer, 1904–1923). In New Zealand he visited Dunedin, Queenstown, Mt. Egmont, Rotorua and Auckland; his collections are widely distributed (see Schultze-Motel, 1982).

During this period several European collectors visited New Zealand. Dr. Henri Filhol (1843–1902) was surgeon, biologist and geologist on the vessel *Vire* as part of the 1874 French expedition to Campbell Island to observe the transit of Venus. The hepatics were reported by Kirk (1882), who lists *Jungermannia monodon* and *Marchantia tabularis*, and possibly by Stephani.

Dr. Sven Berggren (1837–1917; cf. Anon., 1917), a Swedish botanist from the University of Lund and an excellent draughtsman, visited New Zealand during the period of 1 January 1874 – April 1875. The expedition was encouraged and possibly suggested by Lauder Lindsay (Bagnall, 1970a). Bagnall (1970a, 1970b) enumerated portions of Berggren's diary that are relevant to his travels in New Zealand, including notes on localities and dates. Berggren (1898) published a single account of his trip to New Zealand, the excellent "On New Zealand Hepaticae," which included a number of new species (e.g., *Cesia cuspidata* and *C. stricta*, both later transferred to *Gymnomitrion*), as well as excellent descriptions and illustrations. He is commemorated by the names *Chloranthelia berggrenii* (Herzog) R.M.Schust., *Lepidolaena berggrenii* E.A.Hodgs. and *Pachyschistochila berggrenii* J.J.Engel & R.M.Schust.

The German morphologist Karl I. E. Goebel (later Ritter von Goebel, 1855–1932; cf. Bower, 1933; Lloyd, 1935) traveled to New Zealand and Australia in 1898–1899. Goebel accompanied Leonard Cockayne to Westland for two weeks of field work. Cockayne (1933) recalled, "In a moist gully at the base of Mount Alexander in Westland crowned with liverworts of every size and shape (many being giants of the family) von Goebel's delight rose to its highest pitch. 'Here,' he cried, 'were it possible for me, I would build a cottage and spend the rest of my life studying the bryophytes of this gully.'" Goebel was chiefly interested in the form of plant organs in relation to their function and how these concepts may be explained in physiological, morphological and anatomical terms. His investigations included the formation of leaves in liverworts, the form and function of elaters, the dehiscence of antheridia and the

anatomy of the sporophyte capsule (see also comments on fungal components; p. 53). Goebel published major works that were based in part on New Zealand materials that he collected; these publications include *Beiträge zur Kenntnis australischer und neuseelandischer Bryophyten* (Goebel, 1906) and *Organographie der Pflanzen* (Goebel, 1915, 1930). Goebel is commemorated by the names *Goebeliella* Steph. and *Goebelobryum* Grolle.

Early twentieth-century activity

Apart from the continued work of Stephani, little significant activity occurred during the early twentieth century in the area of liverwort collecting and publication. Lilian Gibbs (1870–1925; cf. Godley, 2004; Gibbs, 1911), a British botanist who collected in Africa, New Guinea and Fiji, visited New Zealand in 1907–1908 and collected liverworts at Nihotupu Hills in the Waitakere Range near Auckland and Mt. Te Aroha. Her collections were determined by Stephani and included four new species that Stephani later published; these were *Marchantia laceriloba* Steph., *Aneura papulolimbata* Steph., *Calobryum gibbsiae* Steph. (≡ *Haplomitrium gibbsiae*) and *Lepidozia gibbsiana* Steph. (≡ *Telaranea gibbsiana*). William Henry Pearson (1923a, 1923b) published several new species and provided observations based on the collections from New Zealand of William A. Setchell (1864–1943), an algologist and professor of botany at the University of California, Berkeley); examples are *Frullania setchellii* Pearson and *Riccardia riccioides* Pearson. Theodor Herzog (1880–1961; cf. Grolle, 1961e) of Munich and later Jena, Germany, published several papers that dealt with novelties of New Zealand hepatics, mostly based on specimens sent to him by E. A. Hodgson (e.g., Herzog, 1935, 1938); he is commemorated by, e.g., *Herzogianthus* R.M.Schust., *Herzogobryum* Grolle and *Lepidozia herzogii* E.A.Hodgs. (≡ *Telaranea herzogii*). Alexander W. Evans (1868–1959, Yale University, New Haven) authored several papers that included observations on New Zealand specimens, e.g., on species of *Marchantia* (Evans, 1917), *Metzgeria* (Evans, 1923) and *Acromastigum* (Evans, 1934).

G. Einar Du Rietz (1895–1967), a Swedish botanist, visited New Zealand in 1926 and 1927 and collected extensively in a number of plant groups, e.g., the genus *Euphrasia*, and lichens (see Galloway, 1985, p. xxi). He and his wife Greta Du Rietz collected liverworts on Auckland, Campbell and Antipodes islands in 1927, and Hodgson (1962a) and Hodgson and Sainsbury (1948) published information on these collections.

Mid-twentieth-century activity

Collectors and publishers during the mid-twentieth century included most notably E. A. Hodgson (1888–1983), a resident of Wairoa, Hawke's Bay. Mrs. Hodgson published a number of papers during the period of 1930 to 1972; for a necrology see Godley (1984). Mrs. Hodgson did relatively little field work, and "otherwise she was dependent on other collectors of whom the earliest were K. W. Allison, G. O. K. Sainsbury, J. H. McMahon (Marlborough), V. D. Zotov, Lucy B. Moore, G. Simpson and J. S. Thomson, V. W. Lindauer, Mrs. J. D. Smith (Stewart Island), B. Teague, Ruth Mason, Ella Campbell, and her daughters Lucy and Helen. Later there were her son-in-law, A. P. Druce, Margaret Simpson, William Martin, Jane Taylor, C. J. Burrows, L. Visch and G. A. M. Scott" (Godley, 1984, p. 23). Several collaborators of Mrs. Hodgson are particularly notable. G. O. K. Sainsbury (1880–1957; cf. Martin, 1957; *Radula sains-*

buriana E.A.Hodgs. & Allison), who authored *A Handbook of the New Zealand Mosses* (Sainsbury, 1955), collaborated with Hodgson in many ways, particularly in the very early days of her career as an hepaticologist. Godley (1984, p. 21) remarked that Sainsbury in 1925 wrote to Mrs. Hodgson asking her to collect plant material for him, and "thus began one of the most important friendships in Mrs. Hodgson's life."

The hepatic collections of Victor D. Zotov (1908–1977; cf. Thomson, 1977) of the Plant Research Bureau, Wellington, are mainly from North Island and in particular were gathered from the Tararua and Ruahine Ranges in the 1930s and 1940s; he visited Campbell Island in 1961. His collections were published in various papers by Hodgson (e.g., Hodgson, 1962a on the Campbell Island collections) and some by Herzog (1935). Zotov is commemorated by *Lophocolea zotovii* Herzog (= *Hepatostolonophora rotata*).

A. P. Druce's (1920–1999; cf. Atkinson, 1999) collections of liverworts also were included in several studies of Hodgson's, and he is credited, for example, with making the first collection of the remarkable *Phyllothallia nivicola*, a genus and species described by Hodgson (cf. Hodgson, 1964a). Druce is commemorated by *Pseudocephalozia drucei* R.M. Schust. (≡ *Paracromastigum drucei*).

William Martin (1886–1975; cf. Galloway, 1976) published a number of papers on higher plants, particularly vegetation studies. The *Flora of New Zealand* (Martin, 1961) included several pages devoted to hepatics, and his two papers on "The Bryophytes of Stewart Island" (Martin, 1949, 1950) are noteworthy. He is commemorated by several names, including *Lepidozia martinii* E.A.Hodgs. (≡ *Telaranea martinii*).

A number of individuals spent 12 months at a time on Auckland and Campbell islands during World War II, having been sent there by the New Zealand government as coastwatchers for enemy ships (see Turbott, 2002) after a German ship (the *Erlangen*) refueled at Carnley Harbour (Auckland Island) by cutting rata (*Metrosideros umbellata*) when escaping from New Zealand in 1939. Zoologists, surveyors and meteorologists made up the highly secret Cape Expedition. They were selected for their interests and skills to help occupy the many idle hours available between shifts when on duty at the lookout hut. Cape Expedition staff who collected bryophytes were:

W. H. Dawbin—Auckland Island, 1943. A zoologist who collected many flowering and non-flowering plants.

George Easton ("M. E. Easton" in Hodgson [1962a])—Auckland and Campbell islands, 1944–1945. A surveyor.

Robin L. Oliver—Auckland and Campbell islands, 1944. A zoologist.

Jack H. Sorensen—Campbell Island, 1942, 1943 and 1945. A zoologist and botanist.

E. G. (Graham) Turbott—Auckland Island, 1944–1945. Ornithologist and director of the Auckland Museum (1964–1979). (Turbott visited the Auckland Islands again in 1950.)

The specimens collected by these individuals were made available to Hodgson, who published her "Hepatics from the subantarctic islands of New Zealand including 'Cape Expedition' collections from the Auckland and Campbell Islands" (Hodgson, 1962a).

K. W. Allison (1894–1976; cf. Macmillan, 1978) made important contributions during this period. Allison, a forester who worked for the New Zealand Forest Service at Rotorua, Waipoua and Dunedin, was an avid collector of mosses and liverworts and exchanged materials with Hodgson, with whom he coauthored a number of species. His collection of 7600 hepatics is at CHR. Despite gaining a knowledge of the New Zealand Hepaticae more or less

equal to that of Hodgson through exchange of material with her, he published little independently, but coauthored with John Child *The Liverworts of New Zealand* (Allison and Child, 1975), the second and only reasonably comprehensive account of New Zealand hepatics since Hooker's *Flora of New Zealand*. Allison collected the distinctive hepatic flora of the pumicelands south of Rotorua before they largely disappeared under extensive *Pinus radiata* forests planted from the 1930s onwards.

Raymond E. Hatcher (1930–1967; cf. Fulford, 1968b) traveled to New Zealand as a Fulbright scholar and did field work during the period January 1954 – February 1955. Hatcher authored papers on *Trichocolea* in New Zealand (Hatcher, 1958), a world monograph of *Isotachis* (1960–1961) and several other papers (see Bibliography). Hemstead Castle (1894–1974, Yale University, New Haven) published a number of papers dealing with *Radula*, several involving New Zealand species (see Bibliography).

Jane Taylor (1924–), a student of Margaret Fulford (University of Cincinnati), was research fellow at the Botany Division of the Department of Scientific Research (DSIR) in New Zealand between 1961 and 1963 (Botany Division, 1963) and was interested in *Lepidoziaceae* (especially *Lepidozia*). While in New Zealand she mainly attempted chromosome studies on New Zealand liverworts. Hodgson named *Metahygrobiella tayloriae* E.A.Hodgs. (= *Metahygrobiella drucei*) for her. Her papers are cited in the Bibliography, including the unusual study of spores and elaters of New Zealand taxa that included stereo pairs of scanning electron micrographs (Taylor et al., 1974).

Mid-to-late twentieth-century activity

During the second half of the twentieth century, Rudolf M. Schuster visited New Zealand during the following periods: 1962, 1967, 1969–1970 (Campbell Island), 1983–1984 and 1995. Schuster published many papers based on specimens that he collected. His collections and publications were fundamental in establishing a modern taxonomy for liverworts (see the Bibliography for a list of his contributions to the New Zealand hepatic flora).

Riclef Grolle (1934–2004; cf. Zündorf et al., 2005; Gradstein, 2005) of Jena, Germany, and a student of Herzog, published a number of papers that considerably improved our knowledge of New Zealand hepatics, e.g., on *Kurzia* (1964b), *Herzogobryum* (1966b), *Lepidolaenaceae* (1967a), *Jamesoniella* and *Cryptochila* (1971a), and *Lejeuneaceae* (1973, 1975a, 1980b, 1980c, 1984).

Ella O. Campbell (1910–2003; cf. Rapson, 2004), botany lecturer at Massey University, Palmerston North, published many papers dealing with New Zealand liverworts and hornworts, including detailed morphological studies (see Bibliography for a list of her papers that deal with liverworts).

W. R. Sykes of Botany Division, DSIR, visited the Kermadec Islands in 1966, 1968 and 1970 and collected bryophytes there; these were identified by Ella Campbell (cf. Sykes, 1977).

Bruce Hamlin (1929–1976; cf. Yaldwin, 1976) initially trained under Victor Zotov at the Botany Division, DSIR, Wellington. As botanist at the National Museum, Wellington (1954–1976), he worked on the genera *Uncinia* and *Carex* as well as producing popular books on native trees and ferns, but later he became interested in the liverwort flora and compiled a comprehensive checklist of New Zealand hepatics (Hamlin, 1972, 1973a), as well as several other papers (see Bibliography). Peter Johnson of Botany Division, DSIR, Dunedin, made ca. 2800 collections of hepatics on the Auckland Islands in 1973 on behalf of Hamlin; these are lodged at WELT.

George A. M. Scott (1933–1998; cf. Dalton, 1998) originally from Glasgow, Scotland, took up a lecturing position in 1961 at the Botany Department of the University of Otago. In 1970 he moved to Melbourne to teach at Monash University and then Melbourne University, where he continued his interest in the Australasian hepatic flora (cf. Scott, 1985). He was particularly interested in bryophyte ecology and published a number of papers on New Zealand mosses and hepatics. He is commemorated by *Protomarsupella scottii* R.M.Schust. (≡ *Allisoniella scottii*).

John Child (1922–1984; cf. Olssen, 1998), of Dunedin, was an economist by vocation, teaching at the University of New South Wales and Otago University, and wrote a number of popular books on a wide variety of natural history topics in both Australia and New Zealand, culminating in the noteworthy collaboration with Allison mentioned above. His collections, numbering ca. 5000, are at CHR and F. He is commemorated by *Pachyschistochila childii* R.M. Schust. & J.J. Engel and *Marsupella sparsifolia* subsp. *childii* R.M. Schust. and honored by the annual John Child Bryological Workshop.

John Bartlett (1945–1986; cf. Galloway, 1987), an Auckland school teacher with an exceptional eye for the unusual, collected bryophytes and lichens widely in New Zealand in the period 1981–1986. He is commemorated by *Kymatolejeunea bartlettii* Grolle.

John Engel conducted field work in New Zealand during the periods of 1971, 1982–1983, 1995, 1997, 2003, 2006 and 2007. The 1971 period in New Zealand was prior to participation in an expedition to Kerguelen Island under the auspices of the United States Antarctic Research Program (USARP). Field work involving collection of hepatics as part of the USARP program also was conducted by Rudolf Schuster and Dale Vitt (Campbell Island, cf. Vitt, 1974) and Ralph Common (Auckland Island, December 1972 – January 1973).

Late twentieth and early twenty-first century collectors and publishers include David Glenny and John Braggins, the latter of whom trained several hepatic students at the University of Auckland, e.g., Elizabeth Brown, Matt von Konrat and Matt Renner, with theses on *Riccardia*, *Frullania* and *Radula*, respectively. Rodney Lewington of Wellington is involved in collecting projects, most recently centering on Fiordland.

2. Biogeography of New Zealand's liverwort flora in the world context

The Southern Hemisphere flora

New Zealand (Map 1), with, to date, a flora of 595 liverwort and 13 hornwort species, has a strong representation of a cool-temperate Southern Hemisphere flora that is distinct from the floras of the tropics and the Northern Hemisphere. Examples of genera with a mainly Southern Hemisphere distribution are *Adelanthus*, *Balantiopsis*, *Chiloscyphus*, *Clasmatocolea*, *Gackstroemia*, *Herbertus*, *Heteroscyphus*, *Lepidolaena*, *Marsupidium*, *Pachyschistochila*, *Schistochila*, *Temnoma*, *Triandrophyllum* and *Tylimanthus.* Most of these genera are shared mainly by Australia, New Zealand and South America, but some have a few species in the Northern Hemisphere and/or the tropics. Characteristically, whereas the Southern Hemisphere species in these genera have quite narrow ranges, the species in genera that are also present in the Northern Hemisphere have wide ranges, e.g., *Adelanthus lindenbergianus*, with a distribution that includes the Mascarene Islands, Réunion, Madagascar, South Africa, Uganda, Congo, the Tristan group, South Georgia Island, the Falkland Islands, southern South America, the Andes north to Mexico, western Ireland and northwestern Scotland.

Map 1.
South polar projection showing position of New Zealand relative to other Austral areas.

In contrast to its rich leafy liverwort flora, the Southern Hemisphere is comparatively poor in the complex-thallose *Marchantiales*. Of the 27 genera in this order, Australasia has only 10. *Neohodgsonia*, a monotypic genus of New Zealand, Tristan da Cunha and Gough Island, is the only Marchantialian genus confined to the Southern Hemisphere.

New Zealand is the distributional center of a number of families and genera of *Jungermanniales* and *Metzgeriales* as measured by its relative richness at all taxonomic levels in these groups and by the presence of many isolated species that may be paleoendemics. Examples of this richness and paleoendemism are the families *Lophocoleaceae*, *Schistochilaceae*, *Treubiaceae*, *Trichocoleaceae*, and the genera *Telaranea* and *Zoopsis.* Paleoendemism is exemplified not only by many endemic species without close affinities to other taxa (e.g., *Archeophylla schusteri*, *Dendromastigophora flagellifera*, *Temnoma quadrifidum*, various *Lepidolaena* spp. and various *Lepidozia* spp.), but by isolated endemic genera, especially *Allisonia*, *Echino-*

lejeunea, *Herzogianthus*, *Jubulopsis*, *Lembidium*, *Megalembidium* and *Verdoornia*, all of which lack relatives with close affinities at the genus level.

Endemism

About 50% of the 595 New Zealand liverwort species are endemic. This percentage is about the same as for the ferns (Brownsey, 2001), lower than for the seed plant flora (83% according to Wilton and Breitwieser, 2000), but over twice the number of mosses (23% according to Glenny and Fife, in prep.). This degree of endemism is much higher than for any Northern Hemisphere liverwort flora. For comparison, ca. 20% of Australia's liverwort flora is endemic.

New Zealand has two endemic families, both monotypic: *Jubulopsidaceae*, comprising *Jubulopsis novae-zelandiae*, a twig and bark epiphyte of the Auckland Islands, Stewart Island, Fiordland and Westland (see Engel, 2005b); and *Verdoorniaceae*, comprising *Verdoornia succulenta*, a simple thallose liverwort of the North and South Island penalpine and alpine zones.

New Zealand has 18 endemic genera: *Amphilophocolea*, *Allisonia*, *Bragginsella*, *Castanoclobos*, *Cryptostipula*, *Dinckleria, Echinolejeunea*, *Eoisotachis*, *Herzogianthus*, *Jubulopsis*, *Kymatolejeunea*, *Lamellocolea*, *Lembidium*, *Megalembidium*, *Pseudolophocolea*, *Stolonivector*, *Verdoornia* and *Xenothallus*. Fourteen of these genera are monotypic.

Flora shared with Australia

New Zealand has 49 families, and apart from the two that are endemic, only seven families (*Allisoniaceae*, *Antheliaceae*, *Cephaloziaceae*, *Goebeliellaceae*, *Monocleaceae*, *Phyllothalliaceae* and *Ptilidiaceae*) are not shared with Tasmania or mainland Australia. Of New Zealand's 159 genera and excluding our 18 endemic genera, only 13 genera (*Anthelia*, *Archeophylla*, *Austrolophozia*, *Austrometzgeria*, *Cephalozia*, *Chloranthelia*, *Goebeliella*, *Leiomitra*, *Lepidogyna*, *Monoclea*, *Pachyglossa*, *Phyllothallia* and *Ptilidium*) are not shared with Tasmania or mainland Australia.

Approximately 284 species are in common to New Zealand and Australia, almost all of New Zealand's non-endemic species. Of these, ca. 60 species are exclusively in common to New Zealand and Australia. Examples are the monotypic *Chaetophyllopsis*, which occurs in New Zealand and Tasmania and also Australia (Victoria, Australian Capital Territory, New South Wales, South Australia and Western Australia; see Engel 2005b). *Cephalomitrion* is present in New Zealand, Tasmania and mainland Australia.

By far the largest element exclusively shared with the New Zealand flora is Tasmania. Four genera are shared exclusively: *Brevianthus*, *Eotrichocolea*, *Neogrollea* and *Trichotemnoma*; all are monotypic. About 55 species are shared exclusively by New Zealand and Tasmania. Examples are *Acromastigum cavifolium*, *A. verticale*, *Adelanthus gemmiparus*, *A. occlusus*, *Austrolejeunea olgae*, *Clandarium xiphophyllum*, *Dendromastigophora flagellifera*, *Drepanolejeunea aucklandica*, *Haplomitrium gibbsiae*, *Herbertus oldfieldianus*, *Heteroscyphus cymbaliferus*, *H. decipiens*, *Hymenophyton leptopodum*, *Isolembidium anomalum*, *Lepidolaena clavigera*, *Metzgeria submarginata*, *Pachyschistochila succulenta*, *P. trispiralis*, *Paraschistochila pinnatifolia*, *Plagiochilion conjugatum*, *Radula multiamentula* and *Temnoma pulchellum*. These species are taxonomically spread very evenly across the families and genera. No genera and only a few species are exclusively shared with mainland Australia. These are mostly shared with the southeastern states Victoria and New South Wales (e.g., *Drucella*

integristipula, *Lepicolea attenuata*, *Lepidolaena palpebrifolia* and *Pedinophyllum monoicum*) and may extend into Queensland (e.g., *Telaranea elegans*).

Flora shared with southern South America

Several genera are shared exclusively with southern South America (i.e., *Acrolophozia*, *Archeophylla*, *Austrolophozia*, *Isophyllaria*, *Lepidogyna*, *Pachyglossa* and *Phyllothallia*). *Monoclea* has two species, *M. forsteri* of New Zealand and *M. gottschei* in tropical and subtropical America and warm-temperate regions of Chile and Argentina. Some genera are shared by New Zealand, Tasmania (and in some instances mainland Australia) and southern South America, e.g., *Allisoniella*, *Austrolejeunea*, *Blepharidophyllum*, *Clandarium*, *Gackstroemia*, *Hepatostolonophora*, *Herzogobryum*, *Lepicolea*, *Leptophyllopsis*, *Nothogymnomitrion*, *Wettsteinia*, and of these, one (*Wettsteinia*) extends into Asia. In the case of the seven genera shared exclusively with southern South America, no species within these genera are shared. Species shared exclusively by New Zealand and southern South America are rather few: *Acromastigum cunninghamii*, *Cephaloziella hispidissima*, *Herzogobryum molle*, *Nephelolejeunea taylinayi*, *Riccardia pallidevirens*, *Saccogynidium australe*, *Symphyogyna hymenophyllum* and *Temnoma quadripartitum*. A number of species are shared by New Zealand, Tasmania (and at times mainland Australia) and southern South America, e.g., *Anastrophyllum schismoides*, *Chiloscyphus austrigenus*, *C. bispinosus*, *Clasmatocolea notophylla*, *Cololejeunea pulcherrima*, *Nothogymnomitrion erosum*, *Riccardia crassa* and *Triandrophyllum subtrifidum*. *Metzgeria decipiens* occurs in southern South America, New Zealand, Tasmania, mainland Australia and north to Japan (see map in Engel, 1990a, fig. 85). *Zoopsidella* has an interesting distribution in that most species are present in tropical sectors of South America while the genus is absent in southern South America; one species is shared by New Zealand and New Caledonia.

These various common elements may reflect ancient land connections, or they may suggest very infrequent transoceanic dispersal events across the ca. 6000 km of the Pacific Ocean. Southern South America also has a significant endemic element. The endemic elements at the family level are Grolleaceae and Vetaformaceae, both monotypic (see Engel, 2005b), and at the generic level are *Evansianthus*, *Herzogiaria*, *Nothostrepta*, *Pedinophyllopsis*, *Perdusenia*, *Pigafettoa*, *Pisanoa*, *Pleurocladopsis*, *Pseudolepicolea* and *Roivainenia*.

There is a circumsubantarctic element in the flora in New Zealand, which is present on most subantarctic islands such as Kerguelen Island: *Clasmatocolea humilis*, *Herzogobryum teres*, *H. vermiculare*, *Lepidozia laevifolia* and *Temnoma quadripartitum*. Within New Zealand such species are primarily alpine or are distributed in southern New Zealand as they are cool-temperate species.

Flora shared with the South Pacific islands

Of the Pacific Islands to the north of New Zealand, the strongest affinities are with New Caledonia. Three genera are shared exclusively with New Caledonia (*Austrometzgeria*, *Chloranthelia* and *Goebeliella*). There are 16 species in common but only three of these (*Zoopsis caledonica*, *Frullania chevalieri* and *Goebeliella cornigera*) are exclusive to the two areas; the remainder are also present in Australia (e.g., *Goebelobryum unguiculatum*, *Lethocolea pansa*, *Geocalyx caledonicus* and *Acrobolbus cinerascens*). One species, *Pseudomarsupidium pili-*

ferum, occurs in New Zealand, New Caledonia and in southern South America. Otherwise, the flora in common with the Pacific Islands is composed of widespread tropical species, e.g., *Lejeunea flava* and *L. tumida*.

Bipolar element

A significant bipolar element is present in the New Zealand alpine liverwort flora. These are mostly species that are widespread in northern sectors of the Northern Hemisphere but represented in the Southern Hemisphere in New Zealand (and sometimes also in southern South America): *Anthelia juratzkana*, *Calypogeia sphagnicola*, *Cephaloziella varians*, *Chiloscyphus cuspidatus*, *Lophozia excisa*, *L. bicrenata* (also present in southeastern Brazil), *Marsupella sparsifolia*, *M. sprucei*, *Ptilidium ciliare*, *Scapania nemorosa*, *S. undulata* and *Tritomaria exsecta.*

Minor biogeographical elements

New Zealand has several representatives of a pan–southern-temperate flora, e.g., *Acrobolbus ochrophyllus*, *Bazzania nitida*, *Chiloscyphus semiteres*, *Clasmatocolea vermicularis*, *Cryptochila grandiflora*, *Jamesoniella colorata* and *Marchantia berteroana* are present in New Zealand, Australia, temperate regions of South America and in South Africa (see Engel, 1978, 1990a). To this group also belongs *Hyalolepidozia*, with the generic type (*H. bicuspidata*) in southern South America, the Falkland Islands, Tristan da Cunha and South Africa and an endemic species (*H. microphylla*) in New Zealand. A few species present in New Zealand have distributions that include Australia but also extend into Southeast Asia, e.g., *Marsupidium knightii* and *Metzgeria scobina.*

One species, *Neohodgsonia mirabilis*, is shared by New Zealand and the South Atlantic Ocean islands Tristan da Cunha and Gough.

A small cosmopolitan or subcosmopolitan element is present in the New Zealand flora, almost without exception belonging to the *Marchantiales* and *Metzgeriales*: *Dumortiera hirsuta*, *Fossombronia pusilla*, *F. wondraczekii*, *Metzgeria furcata*, *M. leptoneura*, *Plagiochasma rupestre*, *Reboulia hemisphaerica*, *Riccia bifurca*, *R. crozalsii*, *R. crystallina*, *R. fluitans* and *Ricciocarpos natans*. New Zealand is poor in *Riccia* species (eight species, including three adventive species) and none are common, in contrast to Australia where *Riccia* is a diverse genus of 43 species.

Adventives

New Zealand has only five liverwort species that are believed to be adventive: *Lunularia cruciata* (Campbell, 1965a), *Riccia bullosa*, *R. ciliata* and *R. glauca* (Campbell, 1975, 1977a) and *Marchantia polymorpha*. None of these appear to be abundant or increasing, and only *Lunularia* is widespread in unmodified habitats. This situation is in marked contrast to that for the flowering plants in New Zealand where the number of introduced species exceeds the number of native species. The situation is similar in Australia where only three liverwort species are believed to be adventive (*Marchantia polymorpha*, *Sphaerocarpos texanus* and *Chonocolea doellingeri*).

3. Theories on origins of the present-day New Zealand liverwort flora

Fulford (1951, 1963c) appears to have been the first to propose continental drift as an explanation for the distribution patterns in the temperate Southern Hemisphere liverwort floras. She viewed continental drift as an explanation for the distribution of genera such as *Acromastigum*, *Clasmatocolea*, *Lembidium*, *Lepicolea*, *Neolepidozia* (now placed in *Telaranea*), *Triandrophyllum* and *Bazzania* sect. *Vittatae* that have a mostly New Zealand–Australian–South American distribution but sometimes extend to southern Africa. This view was presented in much greater detail and with many examples by Schuster (1969a, 1972b, 1979b, 1981b, 1982b), who viewed New Zealand's liverwort flora as predominantly a flora of southern and ancient origin. In addition, Schuster (1981b, 1982b) argued that the *Jungermanniales* and *Metzgeriales* had a Gondwanan origin in a consistently cool wet climate, while the *Marchantiales* had a Laurasian origin in a continental climate of wet and dry extremes. Many genera in the *Jungermanniales*, *Metzgeriales* and *Treubiales* show a pattern of distribution with an Australasian–South American–Melanesian concentration of species with a thinning of species in Asia (Schuster, 1982b). For instance, Schuster (1982b) pointed out that 21 of 50–52 families of *Jungermanniidae* are either confined to the Southern Hemisphere or are represented in the Northern Hemisphere by one or two species. Wallace's line is the point at which many of these Southern Hemisphere genera have their limit or become sparse (see Schuster, 1972b). An example of this is provided by the genus *Zoopsis* with eight New Zealand species (six endemic), four Australian species (none endemic) and two Southeast Asian species (one endemic to that region).

This Gondwanan-origin view has been given a strongly vicariance interpretation by some subsequent authors, who interpreted the presence of the same species in New Zealand and Tasmania or New Zealand and southern South America to mean that these species were present in Gondwana 80 Mya and that speciation and mutation rates in the DNA of moss and liverwort genera studied has been especially slow (especially Frey et al., 1998 on the moss *Lopidium*; but also Meissner et al., 1998 on *Monoclea*; Stech et al., 2000 on *Treubia*; Schaumann et al., 2003 on *Symphyogyna*). The concept of "old," "senescent" and stenotypic taxa in the liverworts was put forward by Schuster (1979b) and adopted by Frey et al. (1998), who introduced the term "stenoevolution" for taxa appearing to have very low rates of DNA mutation. McDaniel and Shaw (2003) considered these rates, which are much lower than those reported for any group of land plants, to have a more likely explanation in recent spore dispersal. Heinrichs et al. (2006) argued that their DNA sequence data for *Plagiochila*, the largest liverwort genus, was consistent with a Gondwanan origin for the genus as well as very infrequent long-distance dispersal events.

Van Zanten (1978) found a strong correlation between desiccation-resistance of spores and breadth of distribution in Southern Hemisphere mosses. Van Zanten and Gradstein (1988) experimentally measured the resistance of Neotropical moss and liverwort spores to drying, freezing and ultraviolet light and concluded that the spores of most Neotropical liverworts (including some species present in New Zealand) were insufficiently drought- or ultraviolet-resistant to survive in high-altitude (10–12 km) jet stream winds for the duration of trans-oceanic dispersals, but did not rule out dispersal on more moist lower-altitude winds. Van Zanten (1978) took the view that both long-distance dispersal and vicariance are responsible for present-day distribution patterns. Where genera but not species were shared (as is commonly the case between New Zealand and southern South America), vicariance was the explanation, but where species were shared (as is commonly the case between New Zealand and

Tasmania), long-distance dispersal was responsible. Schuster (1979b) argued that van Zanten's (1978) experimental results implied that transoceanic dispersal of bryophytes should be so common that endemism would be almost nonexistent. He argued that other factors needed to be taken into account to explain observed levels of endemism: (1) whether the spore is unisexual or bisexual, (2) whether asexual reproduction is possible, (3) the habitat of the taxon (e.g., whether the habitat is open to wind) and (4) competition between new arrivals and existing species assemblages. Schaumann et al. (2003) used van Zanten's (1978) data on the lack of freeze and desiccation resistance of *Lopidium* spores as support for their vicariance explanation of the distribution of the genus. Muñoz et al. (2005) presented evidence that bryophyte, fern and lichen distributions in the Southern Hemisphere correlated with "wind connectivity" between islands better than with geographical proximity of islands, but did not consider that wind connectivity may link islands of similar climate.

Schuster (1983, p. 600) concluded that all taxa of the liverwort floras of the Atlantic volcanic islands of 5–20 Mya (Tristan da Cunha, Gough and Nightingale islands) "had to arrive within a geologically limited time span." The same argument applies to New Zealand's subantarctic islands, which are of recent (Miocene to Pleistocene) and of volcanic origin. Their floras, with a total of ca. 175 species, are almost entirely composed of species shared with the main islands of New Zealand and include species that are endemic to the New Zealand botanical region (e.g., *Archeophylla schusteri*, *Lembidium nutans* and *Monoclea forsteri*). The exceptions are two endemic species (*Plagiochila fuscella* and *Riccardia umida*) and one shared exclusively with southern South America (*Riccardia pallidevirens*).

The affinities of the New Zealand flora lie most strongly with its near neighbor, Tasmania. The 2000 km between New Zealand and Tasmania is not incomparable with the 820 km between New Zealand and Campbell Island (although in the case of Campbell Island, the Auckland Islands may have acted as a stepping stone for some species). The two landmasses share an oceanic cool-temperate climate. The climate and landform histories of New Zealand and Tasmania need to be compared in order to explain the persistence and evolution of a Gondwanan liverwort flora throughout the Tertiary in Australasia.

New Zealand's climate and land area were rather different from the present during parts of the Tertiary: the Miocene climate is estimated to have been ca. 10°C warmer, and during the Oligocene New Zealand's land mass was ca. 15% of its present area (Cooper and Cooper, 1995). This accords with the view, now widely held by New Zealand biogeographers, that only a small percentage of New Zealand's vascular species had ancestors in New Zealand that were present at the 80-Mya separation of New Zealand from Gondwana. The implications of these factors for both the continuous presence of a liverwort flora in New Zealand and the composition of that flora throughout the Tertiary have not yet been discussed in the literature.

In the past 10 years, transoceanic dispersal, at least with regard to vascular plants, has gained acceptance as the major source of New Zealand's flora (Pole, 1994; Brownsey, 2001; McGlone et al., 2001; Winkworth et al., 2002; Knapp et al., 2005) even in *Nothofagus*, a much-cited example of vicariance. DNA-based phylogenies of vascular plants have made it apparent that New Zealand has received most of its vascular flora since the Miocene from Australia, South America and the Pacific Islands, and has contributed to those other floras over the same period. The rate of successful dispersal and establishment seems to have been low in many vascular plant genera, as it is common to discover from a DNA-based phylogeny that a genus in New Zealand has radiated from a single arrival.

However, evaluation of the extent of long-distance dispersal as it relates to Austral hepatics must take into account factors inherent to this plant group. Schuster (1984b, p. 602) remarked that "much has been written on long-distance dispersal; I can only reemphasize what

seems obvious: in 'old,' usually stenotypic taxa, such as the subantarctic monotypes (e.g., *Herzogiaria* and *Isophyllaria*), and in such 'relict' taxa as *Dendrobazzania*, lack of both sexual and asexual dispersal devices excludes these taxa from consideration in any discussion of long-distance transport. In such instances, invoking long-distance transport is manifestly absurd and the disjunct ranges are at least in part the result of contraction of formerly more widespread ranges." Moreover, it must be remembered that the liverwort gametophyte is haploid, and that "spores of *Jungermanniae* are produced on low sporophytes attached to low gametophytes: they are produced by plants usually growing in moist and sheltered sites screened from drying winds. Hence opportunity for wind dispersal of disseminules is slightly less than is the case with the taller seed plants" (Schuster, 1969a, p. 49). Also, these concepts must be coupled with the ecological behavior of liverwort taxa. Many occur in sheltered, shaded, permanently moist sites both under alpine and notably also in protected niches within forests (see discussions in Schuster, 1969a, p. 86 and Schuster, 1979b, p. 2182); these niches all or for the most part are not subjected to wind currents relevant to long-distance dispersal. Givnish and Renner (2004, p. 5) aptly addressed these arguments regarding disjunct plant distributions and concluded that such studies "require the judicious use of complementary data on phylogeny, biogeography, ecology, and palaeodistributions in time and space."

4. Ecological provinces of New Zealand

Cockayne (1928) formalized a system of botanical provinces for New Zealand. Wardle (1991) adopted this system but modified the names and boundaries to make them compatible with the system of 85 ecological regions and 268 ecological districts (McEwen, 1987) that is in widespread use in New Zealand.

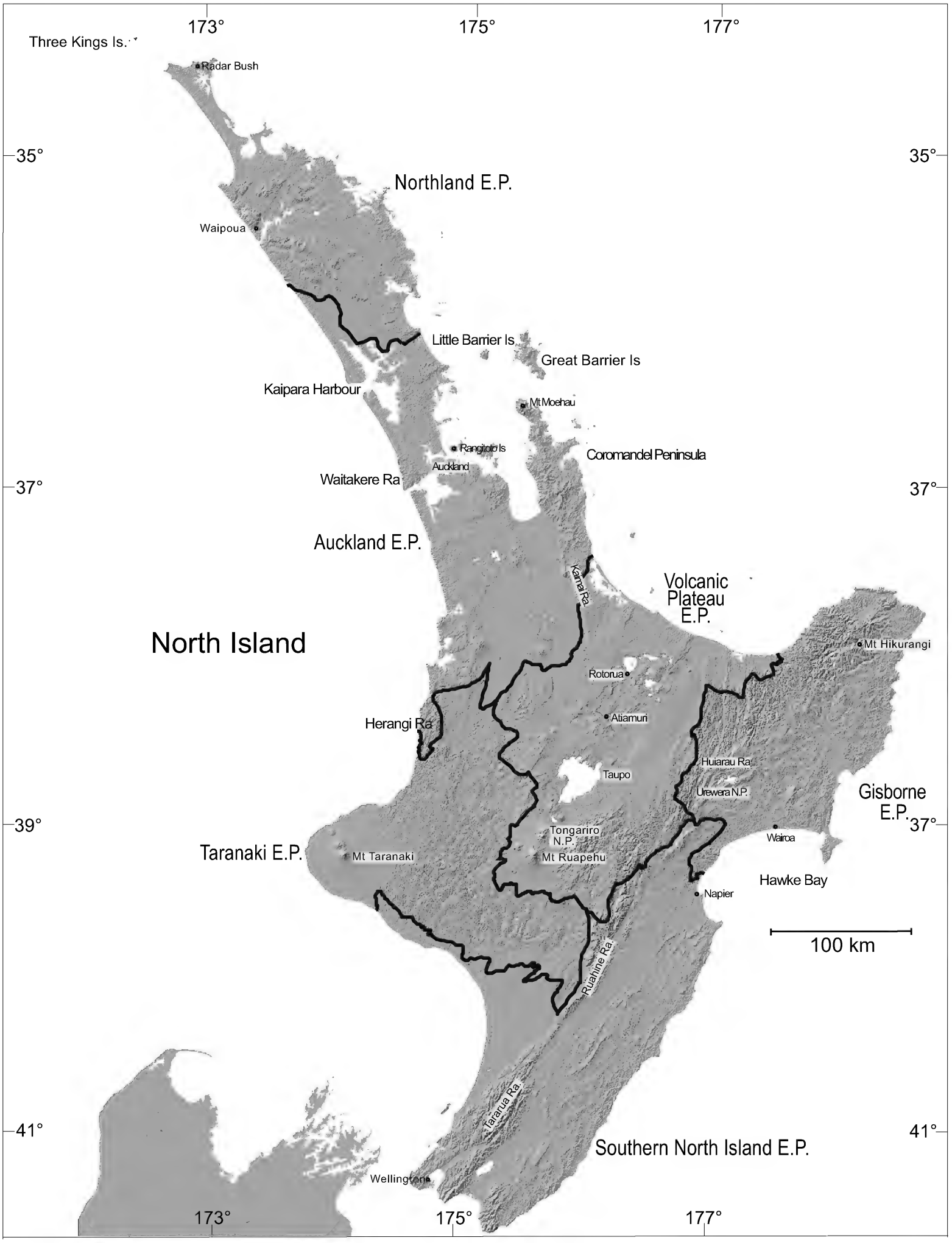
This flora uses Wardle's (1991) botanical provinces and their boundaries (Maps 2, 3), but refers to them as ecological provinces (EPs) to convey that they can be considered part of the hierarchical system of provinces, regions and districts. The system makes more biogeographical sense than the land districts adopted by the *Flora of New Zealand* series (Allan, 1982; Edgar and Connor, 2000; Galloway, 1985; Healy and Moore, 1980; Moore and Edgar, 1970; Webb et al., 1988) and printed on the rear endpapers of each of those volumes, but in some cases (e.g., Canterbury), the names and boundaries are the same.

The ecological regions (ERs) are nested within ecological provinces with the exception of North Westland ER, which is split between Westland and Western Nelson EPs. Wardle's boundary between Westland and Western Nelson EPs is more biogeographically meaningful than the ecological region boundary. An outline of these provinces is presented here, but for more detail see Wardle (1991, chapter 6).

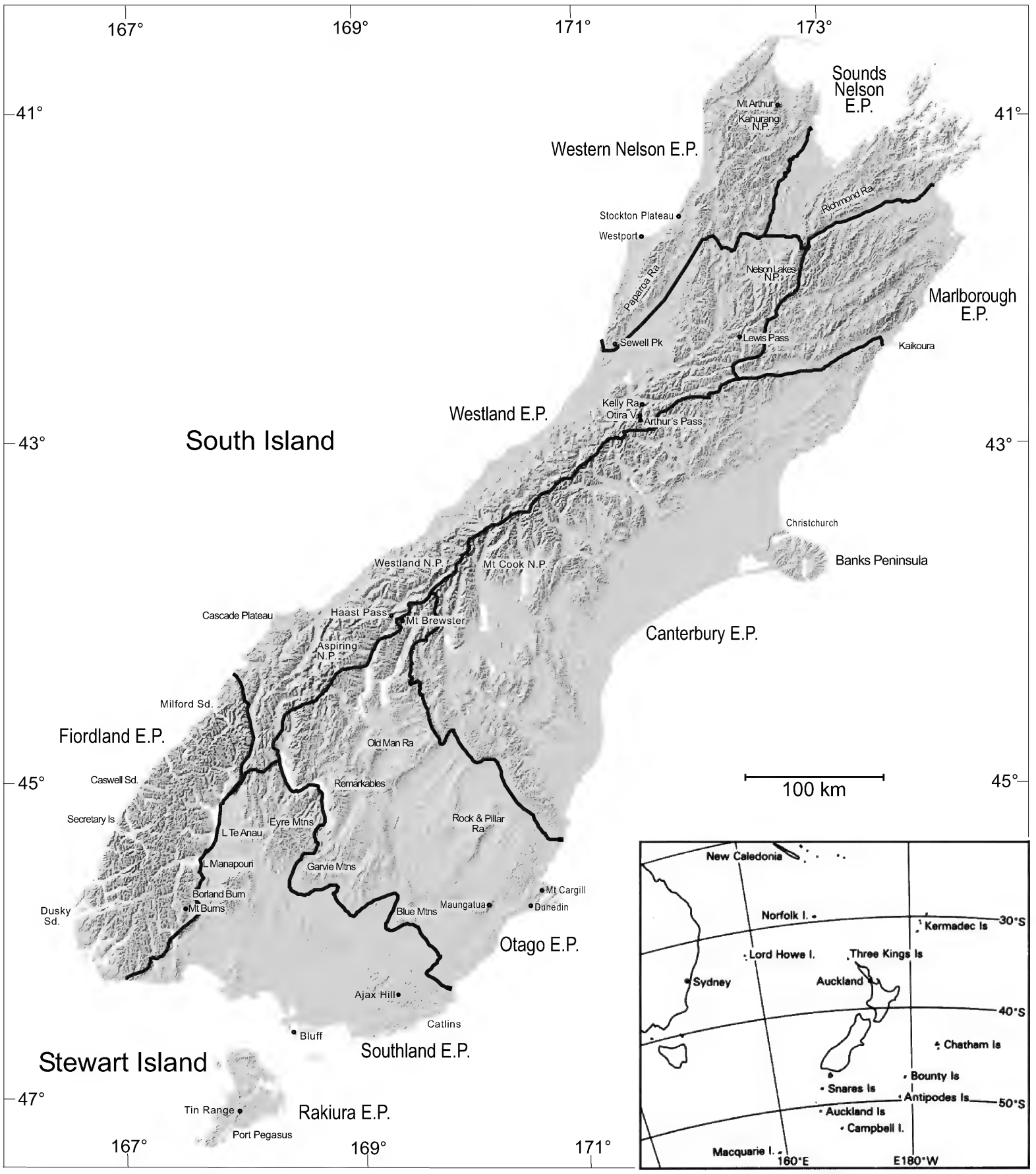
Campbell Ecological Province

The province includes Macquarie, Campbell, Auckland, Antipodes and Bounty islands (Wardle, 1991, fig. 6.1). Macquarie Island is excluded from this flora and the following discussion, as the island lies equidistant between Tasmania and the rest of New Zealand; it is politically part of Australia and included in the *Flora of Australia* series (but not in McCarthy, 2003).

The islands are eroded volcanoes of Miocene to Pleistocene age on a granite basement. They are 460–820 km from New Zealand's South Island at latitudes 47–52° S. The Bounty Is-



Map 2.
North Island of New Zealand showing ecological provinces.



Map 3.
South Island of New Zealand and Stewart Island showing ecological provinces. Inset shows the position of outlying islands.

lands have only one vascular species (*Lepidium olearaceum*; cf. Amey et al., 2007) and probably no bryophyte flora, and are excluded from the following discussion. The islands have a blanket of peat except on coastal cliffs and below the island summits (644 m on the Auckland Islands). The climate is cool but without extreme temperatures (at sea level a mean of 8°C, ranging between 4 and 16°C on the Auckland Islands), sunshine hours are low, and rain falls on most days but is not heavy (annual rainfall is 1.0–1.5 m on the Auckland Islands). The vegetation of the Auckland Islands at sea level is *Metrosideros umbellata* forest, and above 200 m

becomes stunted scrub mixed with *Dracophyllum longifolium* and *Myrsine divaricata*. *Chionochloa antarctica* tussocklands occupy the zone from 200 to 450 m. Near the island summits there are low rush-herbfields of *Carpha alpina*, *Marsippospermum gracile* and *Rostkovia magellanica* with the large herbs *Pleurophyllum hookeri* and *Bulbinella rossii* and many small herbaceous species. *Oreobolus pectinatus–Centrolepis ciliata–Astelia subulata–A. linearis* cushionfields occupy raised bogs at all altitudes. Campbell Island lacks tall forest, and most of the lower slopes of the island are scrub and dwarf forest up to 5 m high of *Dracophyllum longifolium* and *D. scoparium*, with *Myrsine divaricata* and *Coprosma* species. Between ca. 150 and 300 m, *Chionochloa antarctica* tussockland was the original vegetation, reduced by pastoral farming and now occupied largely by tall herbfields. Tall macrophyllous herbs (e.g., *Anisotome latifolia*, *Pleurophyllum speciosum*) and short herbfields occupy the zone between 300 m and the summit at 570 m (McGlone, 2002).

Endemism in the vascular flora of the whole group is 14%. The largest island group, the Auckland Islands, is 630 km^2 in area and has a vascular flora of 233 species, of which 2% are endemic.

There are approximately 175 liverwort species known from the group, with the Auckland Islands having ca. 100 species, Campbell Island ca. 160 species (Schuster, 1979b, p. 2183) and the Antipodes Islands ca. 45 species. Only two liverwort species are endemic, *Plagiochila fuscella* and *Riccardia umida*.

Rakiura Ecological Province

The province is comprised of Stewart Island and offshore islands including the Snares Islands and Solander Island. Stewart Island is at 47° S; Mt. Anglem in the north reaches 980 m high, and Mt. Allen in the south 750 m. The southern two-thirds of the island is granite, and the rest is composed of schist or recent sediments, particularly in the large central Freshwater River swamps. Annual rainfall ranges from 1 m at the coast to 3 m in the mountains. Forests of *Dacrydium cupressinum*, *Metrosideros umbellata* and *Weinmannia racemosa* cover large parts of the island, but extensive areas were burned in association with logging of the *Dacrydium* forests and these areas are now covered mostly in seral *Leptospermum scoparium* scrub and *Empodisma minus* sedgelands. Low forests and scrub of *Dracophyllum longifolium*, *Halocarpus biformis*, *Lepidothamnus intermedius* and *Olearia colensoi* are found in the south. Penalpine cushionfields and tussocklands composed of *Chionochloa lanea*, *C. pungens*, *Donatia novae-zelandiae*, *Dracophyllum politum*, *Hectorella caespitosa* and other species are found on Mt. Anglem, Mt. Rakeahua and the Tin Range. Stewart Island has a vascular flora of 585 species and has 28 endemic species (Wilson, 1987). The northern and southern parts of the island are separated by the Freshwater River valley and are floristically distinct. Endemic liverworts are *Lepidozia serrulata*, *Plagiochila hatcheri* and *Radula parviretis*. Several species are shared with Fiordland, Westland and Western Nelson EPs and have their greatest abundance in southern Stewart Island; these are *Acromastigum verticale*, *Allisoniella scottii*, *Castanoclobos julaceus* and *Eoisotachis stephanii*.

Fiordland Ecological Province

The province is formed by gneiss and granite mountains up to 2000 m high that are deeply incised by glaciers forming wide valleys unchanged in shape since the last glaciation and filled

in places by large lakes and deep fiords. Annual rainfall is 6 m on the west coast, decreasing to 2 m on the province's eastern boundary. Forests, mainly of *Nothofagus menziesii*, *N. solandri* and *N. fusca*, cover most of the province. An extensive tussock zone of several *Chionochloa* species occurs above the treeline. The province has a small number of endemic alpine herbaceous species. A notable 368 liverwort species have been recorded (R. Lewington, pers. comm., 2005), and endemics are *Cephalozia pachygyna* and *Chiloscyphus tuberculatus*; all other species are shared at least with Westland or Rakiura EPs.

Southland Ecological Province

The Livingstone (2000 m), Eyre (2020 m) and Garvie (1600 m) mountains in the north of the province (Mavora ER) are composed of greywacke and similar sandstones with bands of ultramafics. Forests in these ranges are *Nothofagus solandri* and *N. menziesii*, with *Dacrydium cupressinum* forests once common in the lowlands. Low hills and the extensive Southland Plain, now in pasture, form the rest of the province. The Catlins forests in the southeast have the largest remaining areas of forest on low hills (Ajax Hill, 700 m). The province has cool temperatures and low sunshine hours. The Eyre Mountains are a center of endemism for alpine genera such as *Celmisia*, *Aciphylla* and *Ranunculus*, and *Seppeltia succuba* of the Eyre Mountains is shared with Macquarie Island.

Otago Ecological Province

This is a very diverse province extending from the Main Divide mountains, which reach up to 3000 m high in the west with high rainfall and permanent snowfields (Lakes ER), to flat-topped ranges 1700 m high in Central Otago ER, to coastal hills and an eroded Tertiary volcano forming Otago Peninsula, which receives moderate rainfall (Otago Coast ER). Annual rainfall is less than 0.5 m in the central basins but ca. 2.5 m on the range summits and in the west of the province. The province lies almost entirely on a schist basement. Near the Main Divide *Nothofagus* forests predominate, but elsewhere almost none of the original fire-prone *Podocarpus totara–Phyllocladus alpinus* forests remain, and the extensive *Chionochloa rubra* tussocklands that replaced the forests are now occupied by pasture. Endemic vascular species are found in salt-pans in the basins, and a number of cushion-forming species are endemic to the cold, wind-swept central ranges. The liverwort flora is not large, and there are no endemics known, although *Haplomitrium minutum* may have originated there.

Canterbury Ecological Province

Greywacke mountains, which reach 4000 m (Aoraki/Mt. Cook), form the western boundary of the province; they have a high annual rainfall and extensive areas of permanent snow. There is a sharp rainfall transition to drier eastern mountain ranges (annual rainfall 0.9–3.0 m), which are occupied by *Chionochloa macra* and *C. rigida* tussocklands and large areas of bare scree and fellfield in the alpine zone. The extensive Canterbury Plain was formed by river alluvium and was once covered with lowland forests but currently retains virtually no native vegetation. Small areas of Tertiary limestone form low escarpments throughout the province. On the eastern coast, Banks Peninsula is a Miocene volcano that was until recently covered in

lowland forest of *Podocarpus totara*, *Prumnopitys taxifolia* and *Dacrycarpus dacrydioides* emergent over a canopy of, among other species, *Hoheria angustifolia*, *Elaeocarpus hookerianus*, *E. dentatus* and *Griselinia littoralis*. The province has few endemic vascular species, but the most distinctive vegetational element is the mat and cushion plants of the wide gravel riverbeds, mountain screes and fellfields. Most of the province's liverwort species are recorded from the wetter western edge of the province. *Andrewsianthus hodgsoniae*, *Bragginsella anomala* and *Cephaloziella pellucida* are endemic; all are found in the alpine zone in the west of the province.

Chatham Ecological Province

Chatham Island (950 km^2) and several smaller islands 860 km from the South Island, all low in elevation (to 290 m), are composed of mid-Tertiary to Pleistocene volcanics interbedded with marine sediments that include limestone. Rainfall is low (ca. 0.8 m per year) and droughts are common in the summer, but peat soils nevertheless cover the southern tablelands of Chatham Island, which have the largest remaining area of forest of *Coprosma chathamica*, *Dracophyllum arboreum*, *Melicytus chathamicus*, *Myrsine chathamica* and *Dicksonia squarrosa*. The province has a vascular flora of 320 species, of which 10% are endemic, including many of the tree species, whose relatives are mostly New Zealand shrub species. There are ca. 155 liverwort species known from the province, none of which is endemic. The most conspicuous element of the flora is a lowland, warm-temperate element, e.g., *Bazzania tayloriana*, *Cryptochila nigrescens*, *Harpalejeunea filicuspis*, *Lamellocolea grandiflora, Nephelolejeuna conchophylla* and *Trichocolea hatcheri*. Most habitats of Chatham Island, including the southern tableland forests, are strongly disturbed by browsing animals. Collections have not been made from the smaller islands of the group.

Westland Ecological Province

The Hollyford Valley and Martins Bay form the southern boundary, while in the north the province includes Nelson Lakes National Park. Most of the province consists of the high mountains forming the Southern Alps, and annual rainfall in these mountains is very high (up to 14 m in the central Whataroa ER) and falls torrentially during storms from the northwest. Flat coastal land up to 10 km wide borders the province and is composed of alluvium and glacial outwash. The same alluvial and glacial landforms are found in the large Grey River valley. Both areas were formerly occupied by tall podocarp forest dominated by *Dacrydium cupressinum*, which was almost completely milled during the twentieth century. In the central region of the province, Whataroa ER, *Nothofagus* is completely absent and the montane forests are composed of *Weinmannia racemosa*, *Quintinia serrata* and *Metrosideros umbellata*. To the north and south of Whataroa ER, *Nothofagus fusca*, *N. menziesii* and *N. solandri* form the forest canopy or are mixed with *Weinmannia racemosa*, and the treeline is formed by *Nothofagus menziesii* or *N. solandri*. There is an extensive penalpine zone above the treeline with a scrub composed of *Dracophyllum* and *Olearia* and *Chionochloa* tussocklands, which gives way to alpine herbfields, open rock and snowfields. The province has no vascular endemics. Endemic liverworts are *Cephaloziella grandiretis*, *Lophozia autoica* var. *alpina*, *L. nivicola* and *Telaranea pennata.* Other species are shared with Fiordland and/or Western Nelson EPs, e.g., *Hygrolembidum triquetrum* and *Lejeunea cyanophora*.

Western Nelson Ecological Province

The province comprises North-west Nelson ER and the part of North Westland ER that includes Denniston and Stockton plateaus and the Paparoa Range. The province has moderately high rainfall (1.7–2.5 m annually) and consists mostly of mountains with deep river gorges and rounded summits to 1500 m. Granites predominate, but the province contains Ordovician-age marbles on the eastern side, Tertiary limestone in the Paparoa syncline, and Tertiary quartzose sandstones on the Denniston and Stockton plateaus north of Westport. Forests of *Nothofagus fusca*, *N. menziesii*, *N. solandri* and *Weinmannia racemosa* predominate, but in the Paparoa syncline some dense lowland podocarp forests of *Dacrydium cupressinum* remain. Above treeline, *Chionochloa pallens* and *C. australis* tussocklands predominate. The Denniston and Stockton plateaus are dominated by seral *Leptospermum scoparium* scrub. The province is floristically the richest in New Zealand for vascular plants as a result of its variety of substrate types and because the area has served as a glacial refugium. *Riccardia alcicornis*, *R. intercellula*, *R. pseudodendroceros*, *Herzogianthus sanguineus*, *Austroscyphus nitidissimus* and *Cephaloziella aenigmatica* are endemic to the province. The province has species shared with Rakiura EP, e.g., *Acromastigum brachyphyllum* and *A. verticale*, and the bryophyte floras of the Denniston and Stockton plateaus have affinities with the Tasmanian flora (e.g., *Neogrollea notabilis*).

Marlborough Ecological Province

The northern boundary of the province is the Wairau River, and the southern boundary lies just south of the Seaward Kaikoura Range and the Hamner Range. The province includes the Seaward and Inland Kaikoura mountains, the Raglan Range and other ranges up to 3000 m in elevation. The annual rainfall is low, ca. 0.6 m in the central part of the province; there is no permanent snow as a result of warm summer temperatures. With the exception of low escarpments of limestone and other marine sediments near Kaikoura, the geology is greywacke, which under such a dry climate forms extensive screes and fellfields. The most distinctive vascular flora of the province belongs to these screes and fellfields, and to the presence of limestone. The liverwort flora is small and has no known endemics.

Sounds–Nelson Ecological Province

The province is composed of two regions: Nelson ER, an extensive sheet of glacial outwash, the Moutere gravels, dissected into low hills (500–200 m) and a coastal alluvial plain; and Richmond ER, comprised of mountains up to 1750 m cut mostly from schist, and including the drowned river valleys of Marlborough Sounds (Mt. Stokes, 1200 m), as well as a number of small islands in Cook Strait that preserve a fauna and flora once present throughout New Zealand. The annual rainfall is low, 0.9 m at Nelson city, and sunshine hours are high. The province is the southern limit for some otherwise North Island species, e.g., *Beilschmiedia tawa* and the epiphytic moss *Braithwaitea sulcata.* Tall podocarp forests once occupied alluvial plains and fans but are rare now, while the hills and mountains support *Nothofagus* forests. There is a small endemic flora of alpine herbs on the Richmond Range. No endemic liverworts are known.

Southern North Island Ecological Province

The province includes the Manawatu Plain, a sandy coastal plain, the narrow Tararua and Ruahine ranges, and the Wairarapa and Hawke's Bay plains and low hills. Extensive lowland forests in the Wairarapa and Hawke's Bay were milled and burnt, and the lowland areas on both sides of the axial ranges are largely covered in pasture. The axial ranges themselves are covered in *Nothofagus* forest at higher altitudes and mixed *Dacrydium cupressinum*, *Knightia excelsa* and *Beilschmiedia tawa* forest at lower altitudes. Above treeline, *Olearia colensoi* scrub and *Chionochloa flavescens* tussockland dominate, but there is no alpine zone. Endemic vascular species are few, as the middle of the province has a floristic gap caused by submergence of most of the area until the late Quaternary uplift of the Ruahine and Tararua ranges. Endemic liverworts are *Pachyschistochila papillifera*, *Cephaloziella nothogena* and *Triandrophyllum symmetricum*.

Taranaki Ecological Province

The province is composed of two distinct areas: Egmont ER that includes the recently active and very young volcano, Mt. Taranaki (2500 m), its extensive ring plain, and two older eroded volcanoes forming the Pouakai and Kaitake ranges; and Taranaki ER, a large area of dissected low hills of Tertiary marine mudstone. Annual rainfall is ca. 1.5 m near the north Taranaki coast, but rises to 6.5 m at 1000 m on Mt. Taranaki, with torrential rain at times. Annual mean temperature is ca. 13°C at New Plymouth, declining to 9°C at 850 m (Clarkson, 1986). Mt. Taranaki has forests of *Dacrydium cupressinum*, *Metrosideros umbellata* and *Weinmannia racemosa*; *Nothofagus* is absent. The remaining inland forests of Taranaki ER are mainly *Beilschmiedia tawa* and *Knightia excelsa*, with patches of *Nothofagus solandri* and *N. truncata* forest on ridges.

Mt. Taranaki is too recent and too recently disturbed to support a diverse liverwort flora despite its high rainfall. Taranaki ER is bryologically poorly known. *Allisoniella recurva* is endemic to the province.

Gisborne Ecological Province

This is a province of mountain ranges, for the most part forested to their summit ridges, with a high point at Mt. Hikurangi (1750 m). The province is fringed by small coastal plains and low coastal hills, with annual rainfall only 1 m. The mountains are composed of greywacke, and the hills in the east are composed of Tertiary sandstones and mudstones, but rhyolite ash up to 3 m deep forms the soils in the Urewera forests. Forests at low altitudes are mostly *Dacrydium cupressinum* and *Metrosideros robusta* emergent over *Dysoxylum spectabile*, *Beilschmiedia tawa*, *Laurelia novae-zelandiae* and *Litsea calicaris* under an annual rainfall of 1.5–2.0 m. Dense tall podocarp forests of *Dacrydium cupressinum*, *Prumnopitys taxifolia*, *Podocarpus totara* and *Dacrycarpus dacrydioides* once filled valley floors on thick ash deposits but have survived logging only at Whirinaki. The Urewera Ranges have *Nothofagus menziesii* on their ridges, under an annual rainfall of 3 m. The forests experience strong disturbance from rain and wind accompanying tropical cyclones. *Petalophyllum hodgsoniae* is endemic to the province.

Volcanic Plateau Ecological Province

The province includes the central volcanoes of Tongariro National Park, including Mt. Ruapehu (2800 m), and the area, mainly to the northwest and extending to the Bay of Plenty coast, that was blanketed by ash showers from these central volcanoes and the huge Lake Taupo caldera in the recent past. A second volcanic center exists near Rotorua, which also distributed ash as recently as 1886 and has thermally heated ground and fumeroles (Clarkson et al., 1991).

Mt. Ruapehu has *Nothofagus solandri* forest on the western side under an annual rainfall of 2.0–3.0 m. *Chionochloa rubra* tussockland is extensive, a result of burning of forest in prehistoric and historical times. The alpine flora is sparse due to the recency of the volcanoes and the area's remoteness from sources in the South Island. The remainder of the province has forests mainly of *Beilschmiedia tawa*, *Laurelia novae-zelandiae* and *Knightia excelsa*, with *Weinmannia racemosa* at higher altitudes; *Dacrydium cupressinum* was common in these forests before logging.

The province has a rich liverwort flora, which is expected due to its catastrophic volcanic activity. This suggests that destruction of forest habitats was never complete even on the slopes of Mt. Ruapehu itself. Species occur on Mt. Ruapehu that otherwise would have their northern limits in the South Island, e.g., *Archeophylla schusteri*, *Diplophyllum gemmiparum* and *Xenothallus vulcanicolus*. The tephra plains around Rotorua had extensive seral *Leptospermum scoparium* and *Kunzea ericoides* shrublands that resulted from Maori burning of forests. These and fire-induced *Dracophyllum subulatum* shrublands on valley floors were probably rich in liverworts including *Chaetophyllopsis whiteleggei* and *Lophozia herzogiana*, but are now converted to either pine plantation or pasture. Other endemics are *Schistochila pellucida* (in the ignimbrite-walled river gorges), *Anastrophyllum papillosum*, *Cephaloziella invisa*, *C. muelleriana*, *C. nothogena* and *C. crassigyna.*

Auckland Ecological Province

This is a province of diverse elements: Waikato peat domes and swamps, now very reduced in extent by draining and burning; Waitakere and Hunua ranges (500 m), on greywacke; Coromandel Peninsula with high points Mt. Moehau (900 m) and Mt. Te Aroha (960 m) on the Kaimai Range, a range of Tertiary volcanoes; and Tainui ER with a karst landscape. A recently active field of volcanoes is present in Auckland city (including Rangitoto Island, 260 m, still covered in forest). Both north and south of Auckland, the low hills once had a mosaic of kauri forest (*Agathis australis*), forest of emergent tall podocarps and *Metrosideros robusta*, and a canopy composed of a variety of dicotyledonous trees (*Beilschmiedia tawa*, *B. tarairi*, *Weinmannia*, *Knightia* and locally *Nothofagus* on the ridges). *Plagiochila bazzanioides* is endemic. Mt. Moehau is special in the province for having a liverwort flora that has many species in common with Western Nelson, Westland and Rakiura EPs, e.g., *Mnioloma novae-zelandiae*; it is also the northern geographical limit for ca. 20 flowering plant species.

Northland Ecological Province

Comprising the area north of Kaipara Harbour, the province notably includes Waipoua Forest in Western Northland ER and the distinctive subtropical area at the northern tip of the North Island, Te Paki ER. The province has a warm-temperate climate, and kauri (*Agathis australis*)

forests dominate the uplands (to 780 m) on infertile podzolized soils. However, where kauri is absent, forests have *Dacrydium cupressinum* emergent over a canopy formed by, e.g., *Metrosideros robusta*, *Elaeocarpus dentatus*, *Weinmannia sylvicola*, *Beilschmiedia tarairi* and *B. tawa*. Typically valleys are dominated by broadleaf species of *Beilschmiedia tarairi*, *Dysoxylum spectabile*, *Corynocarpus laevigatus* and *Vitex lucens*, with tree ferns and *Rhopalostylis* common in the understory. Coastal forest is dominated by *Metrosideros excelsa*. Waipoua, on the western, wetter side of the province, has a rich liverwort flora. *Schistochila nitidissima*, *Frullania wairua*, *Telaranea granulata*, *Cololejeunea falcidentata* and *Rectolejeunea denudata* are endemic to the province. A number of subtropical species extend no further south than Northland, e.g., *Dumortiera hirsuta* and *Stenolejeunea acuminata*. The Three Kings Islands are included in the province and 19 liverwort species have been recorded there, none of which are endemic to the islands (Braggins, 1987).

Kermadec Ecological Province

This province is a group of Pleistocene-age volcanic islands situated 980 km north of the North Island at 29° S in the subtropical zone. Raoul is the main island, 33 km^2 in area and 520 m high, and is volcanically active (as recent as March 2006). It has a vascular flora of 113 species, 10% of which are endemic. *Metrosideros kermadecensis* forms the forest canopy on Raoul Island and formerly did the same on Curtis and Macauley islands. Twenty liverwort species are present (Sykes, 1977), with *Plagiochila pacifica* and *Radula cordiloba* subsp. *erigens* the only endemics. *Plagiochila kermadecensis* is shared with Auckland EP. The province has a subtropical element, e.g., *Archilejeunea planiuscula*.

5. The climate of New Zealand

New Zealand is positioned in the largely land-free South Pacific Ocean mainly in the latitude zone termed the "roaring forties" for its strong westerly airstreams that are not much interrupted by land masses. Westerlies reaching New Zealand are little modified by the land mass of Australia because of the 2000-km-wide Tasman Sea that separates the two countries and because of New Zealand's more southern latitude. Rainfall on the western side of the three main islands is high due to the blocking of the prevailing westerlies by the main mountain axis, the effect being strongest in the central South Island where the mountain ranges are highest. East of the axial mountain ranges annual rainfall decreases rapidly. The highest recorded rainfall for a 12-month period in the central Southern Alps, in the Cropp River valley, was 18 m, but the site with the highest mean annual rainfall is Milford Sound, Fiordland, with 6.7 m per year; the site with the lowest rainfall is Alexandra, Central Otago, with 0.36 m (NIWA science, 2006).

The country occupies the warm-temperate and cool-temperate zones. The Kermadec Islands are in the subtropical zone, but their vegetation is New Zealand warm-temperate in character. At sea level, the entire North Island and northern part of the South Island occupy the warm-temperate zone (mean January air temperature at sea level 17.5–20°C), while most of the South Island and the subantarctic islands occupy the cool-temperate zone (mean January air temperature at sea level 10–17.5°C).

An altitudinal zonation system of lowland, lower montane, upper montane, penalpine and alpine corresponds to these temperature-based zones. The scheme of Wardle (1991, fig. 5.2)

is followed here (Fig. 1), but we avoid the confusing term "subalpine" to refer to forests below treeline. Instead we use the term "upper montane" for forests in the zone below the treeline in accordance with international usage, particularly in the tropics (e.g., Whitmore, 1975, p. 199). These are mostly stunted *Nothofagus solandri* and *N. menziesii* forests, but where beech is absent, e.g., in Central Westland, forest comprised of *Dracophyllum traversii*, *Olearia ilicifolia*, *O. lacunosa*, *Libocedrus bidwillii*, *Archeria traversii* and *Halocarpus biformis* occupies this zone, and on Mt. Taranaki, of *Libocedrus plumosa*, *Podocarpus hallii*, *Griselinia littoralis* and *Olearia colensoi* (Clarkson, 1986). In New Zealand the use of Wardle's term "penalpine" for the zone of tall shrubs and tussocks above the treeline is increasing and seems useful to refer to what in New Zealand is a distinct vegetation zone while avoiding the confusion that exists with the term "subalpine." The tall shrubs of this zone are mostly *Dracophyllum* (especially *D. longifolium* and *D. rosmarinifolium*) and *Olearia* (*O. colensoi*, *O. lacunosa* and *O. ilicifolia*) and the tall tussocks mainly *Chionochloa pallens*, *C. flavescens* and *C. rubra.*

In this scheme, at 43° S, the latitude of Arthur's Pass, lowland forests extend from the coast to an upper limit at 400 m, lower montane forests extend to ca. 800 m and upper montane forests extend to treeline at 1300 to 1350 m (depending on aspect). The penalpine zone at this latitude is between 1300 and 1500 m, and the alpine zone between 1500 and 2000 m (Fig. 1). Wardle (1991) defines a nival zone for areas of permanent snow above this, but we do not refer to this zone since the highest liverwort records are only slightly above the 2000 m level (*Diplophyllum gemmiparum*, 2025 m, *leg. Engel and Braggins* [Engel and Merrill, 1998]).

High and consistent rainfall and cool temperatures on the western side of the islands (particularly in Western Nelson, Westland and Fiordland EPs) result in impressively luxuriant bryophyte growth, with liverworts dominating the bryophyte component of the vegetation on

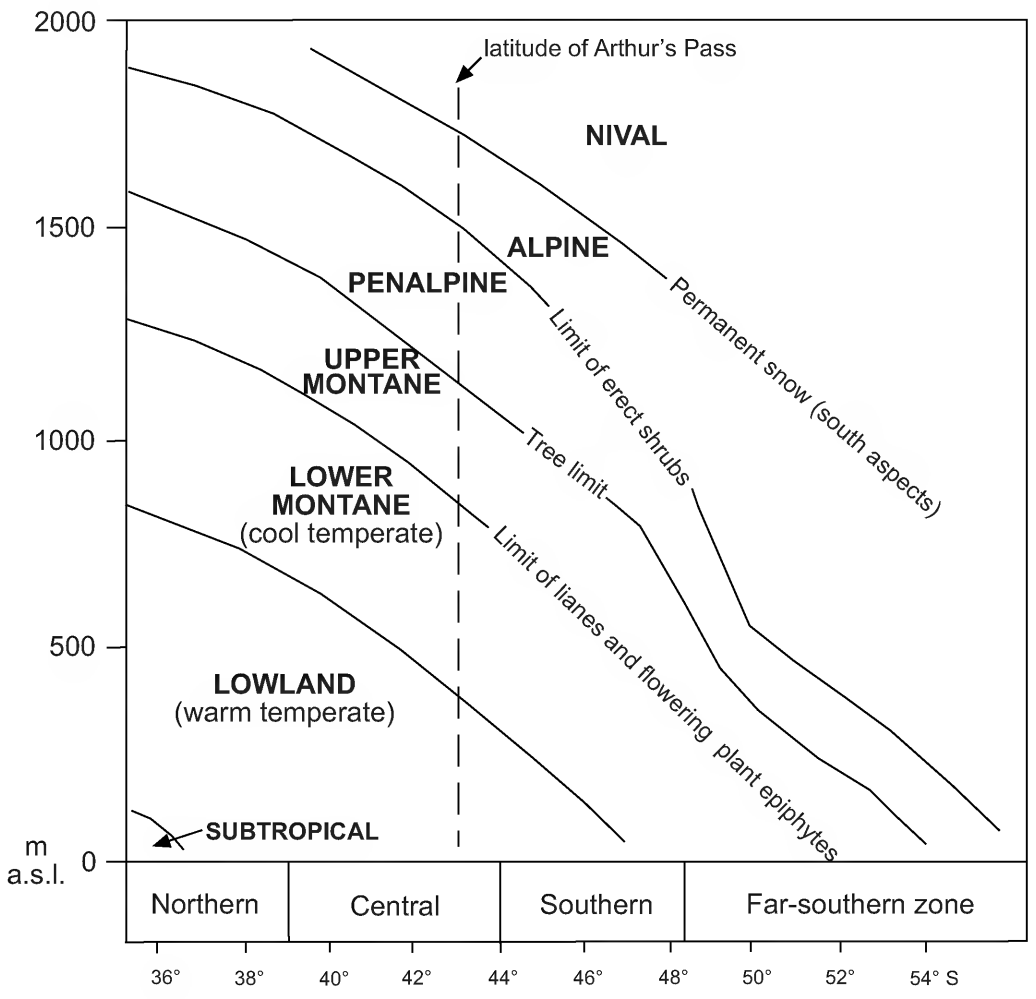


Fig. 1.
Altitudinal belts and their variation with latitude within New Zealand. Adapted from Wardle (1991, fig. 5.2).

the western side of the islands and on Stewart Island. In the western provinces, bryophytes cover a large percentage of the floor of lower and upper montane forests and can be a high percentage of their plant diversity. Some genera that can dominate the ground cover in these areas are *Acromastigum*, *Bazzania*, *Chiloscyphus*, *Heteroscyphus*, *Lepicolea*, *Lepidozia*, *Lepidogyna*, *Plagiochila*, *Riccardia*, *Schistochila*, *Telaranea*, *Trichocolea* and *Tylimanthus*. In eastern provinces where annual rainfall is much lower and summer temperatures reach 30–35°C, mosses dominate the bryophyte component of the vegetation, the bryophyte ground cover is usually less, and there are a limited number of dry-tolerant liverwort species (e.g., *Chiloscyphus bispinosus*, *C. echinellus*, *C. lentus*, *C. semiteres*, *C. subporosus*, *Lepidozia laevifolia* and epiphytes *Frullania aterrima*, *F. deplanata*, *F. monocera*, *F. pentapleura*, *F. patula*, *F. rostrata*, *Lejeunea flava*, *Lepidolaena taylorii*, *Metzgeria flavovirens*, *M. furcata* and *Porella elegantula*). However, constantly moist habitats near streams and in shaded gullies support a wider range of species such as *Asterella tenera*, *Hymenophyton flabellatum*, *H. leptopodum*, *Monoclea forsteri*, *Plagiochila banksiana*, *Radula buccinifera* and *Symphyogyna hymenophyllum*.

6. Geology and landforms of New Zealand

The most notable feature of New Zealand's geology is its position at the junction of the Australian and Pacific tectonic plates. A transform fault, the Alpine Fault, runs through both main islands and has longitudinally offset the two halves of the South Island by 480 km over the last 25 My in which it has been active. However, it is doubtful whether this transform fault has produced disjunctions in plant distributions; none have been detected in the liverwort flora.

The Southern Alps of the South Island and axial mountains of North Island (the Tararua and Ruahine ranges) result from upward movement on the western edge of the Pacific Plate, which is overriding the Australian Plate. They are composed mainly of marine siltstones and mudstones of Mesozoic age, known in New Zealand as "greywacke." Their main physical feature is a tendency to fracture through faulting and freeze-thaw cracking. At high altitude in Canterbury and Marlborough, the shattering of the rock has resulted in extensive bare screes and fellfields. In Westland and Central Otago the same sediments were pressure-metamorphosed and occur as more durable schists. These greywackes and schists are unremarkable in their chemistry. The main effect of the Southern Alps and the axial ranges of the North Island is through the impact these mountains have on the rainfall as discussed above, and the cooler temperatures at higher altitude.

All Tertiary marine limestones occur at lowland to montane elevations and are found at Waitomo, Canterbury and Western Nelson (Paparoa syncline), but also are scattered through other areas, e.g., Southland and Wairarapa. A number of bryophyte species are confined to this rock type and include *Chiloscyphus calcareus* and *Temnoma angustifolium*. Characteristic communities of liverworts occur on limestone walls, particularly in river gorges (e.g., *Asterella australis*, *Heteroscyphus triacanthus* and *Marchantia foliacea*).

Weakly indurated calcareous siltstones called "papa" are common in the lower North Island and are exposed there in large road cuttings. Where there is shade and water seepage these support a distinctive flora and are the exclusive habitat of the hornwort *Phaeoceros coriaceus*.

Marble of Ordovician age occurs mainly in Western Nelson, forming the Arthur Range and Marino Mountains. Pure calcareous soils in these ranges are rare so that only epilithic bryophytes experience high calcium and magnesium concentrations. No liverwort species are known to be special to this substrate. However, sinkholes in these two ranges provide con-

stantly cool and moist conditions, an ideal habitat for species such as *Allisonia cockaynei*, *Haplomitrium ovalifolium* and *Phyllothallia nivicola* (although these species are not restricted to this area or type of habitat).

Ultramafic bands of rock occur in Sounds–Nelson (Richmond Ra.), Otago (Livingstone Mountains) and Westland (Cascade moraine) EPs and consist mainly of weathered serpentine. The rock and derived soils are rich in calcium and magnesium but low in nitrogen and phosphorus. *Nothofagus* forests originally occupied these areas, but they are now largely bare or have *Leptospermum scoparium* scrub. The liverwort flora of these zones is sparse. Dry-tolerant *Chaetophyllopsis whiteleggei* is recorded from the Nelson ultramafic area, and *Castanoclobos julaceus* from the Cascade ultramafic moraine (Westland).

Rhyolite ash (tephra) and ignimbrite (hot aerial ash fused on deposition into a rhyolitic rock) blanket all of Volcanic Plateau EP, most of Taranaki EP and parts of Gisborne and Southern North Island EPs. Most of the material originates from the Taupo, Rotorua and Okataina calderas that were active over the last 0.4 My. The volcanoes of Mounts Tongariro, Ngauruhoe, Ruapehu and Taranaki have produced cones 2000–3000 m high during the last 0.5 My and have added to the ash cover of these provinces. The largest ash shower, ca. 800 km^3 in volume, originated from the first eruption of the Taupo caldera 27,000 years ago. The tephra soils are deep, friable and free draining but not particularly fertile. Ignimbrite is exposed on cliffs and in river gorges. Heated ground and thermal vents near Rotorua have a distinctive bryophyte assemblage; the moss *Campylopus capillaceus* is an endemic of such sites, and *Lepidozia* and *Telaranea* species are common, but there are no liverwort species special to these areas.

Volcanoes are present in other parts of New Zealand, notably the Auckland volcanic field (recently active), Banks Peninsula (Pleistocene), the subantarctic islands (Miocene to Pleistocene), Otago Peninsula (late Miocene to Pliocene) and in Northland and the Coromandel Peninsula (Pliocene). The aa lava present on Rangitoto Island has created the most distinctive environment present on any New Zealand volcano and provides a habitat for a diverse bryophyte flora.

Granites make up almost all of Fiordland, most of Stewart Island and isolated batholiths in Westland (e.g., the Hohonu Range) and are present in Western Nelson EP (e.g., the Paparoa Range). All experience high rainfall and have well-developed peat soils because of the poor drainage and lack of mineral soil development. All have rich bryophyte floras that are associated with these organic soils rather than with the granite substrate itself. The exception is on Stewart Island where there are liverworts that grow mainly on the bedrock itself, kept moist by constant seepage over the rock surfaces (e.g., *Eoisotachis stephanii*).

Extensive lowland alluvial floodplains are present in all provinces of the main islands, particularly the large Canterbury Plains, and have the most fertile soils and mesic climates found in the country. These floodplains were, until human arrival 500 years ago, covered by tall podocarp forests that now exist only in small areas.

7. The vegetation of New Zealand

Forests

Tall conifer forests of the lowlands were once widespread in large areas on alluvium, tephra plains, glacial outwash terraces and estuarine flats, and were often a mixture of *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Podocarpus totara*, *Prumnopitys ferruginea* and

P. taxifolia. Composition varied with soil fertility, drainage conditions and altitude. *Dacrydium cupressinum* is the most common of the tall podocarps in New Zealand and is common as an emergent in forests dominated by *Nothofagus*, *Weinmannia* and *Beilschmiedia*. In Northland and Auckland EPs, *Agathis australis* forest was a major lowland forest type, particularly on old infertile (gleyed and podzolized) soils, often with *Gahnia xanthocarpa* and *Astelia trinervia* forming an understory. In some places *Agathis australis* is emergent over a canopy of *Beilschmeidia tawa* or *B. tarairi*. In fertile and often swampy sites, *Dacrycarpus dacrydioides* forms pure stands (in wet sites associated with *Phormium tenax*), but also occurs on well-drained soils with a *Coprosma* understory. Forests of *Prumnopitys taxifolia*, *Podocarpus totara* and *P. hallii* were common in prehuman times on dry, fertile, well-drained sites such as the Canterbury Plains. On the deep tephra soils of the Volcanic Plateau EP, dense mixed forests of *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Podocarpus totara*, *Prumnopitys ferruginea* and *P. taxifolia* were common; this type of forest is now confined to small areas at Whirinaki, Tihoi and Pureora. Tall podocarp forests have a rather poor terrestrial bryophyte flora due to low light conditions on the floor, but on forest margins or where the canopy is less dense, the epiphytic flora is well developed.

Lowland and montane forests of the warm-temperate zone are a complex and varied assemblage of tree species, mainly *Dacrydium cupressinum* and *Metrosideros robusta* as emergents over a canopy of *Beilschmiedia tawa* (Auckland to Nelson), *B. tarairi* (Northland and Auckland EPs), *Phyllocladus trichomanoides* and *Weinmannia sylvicola* (Northland), *W. racemosa* (south of Auckland), and throughout the North Island, *Knightia excelsa*, *Elaeocarpus dentatus* and *Weinmannia racemosa*. Less widespread and common species that form the canopy are *Ackama rosifolia*, *Corynocarpus laevigatus*, *Dysoxylum spectabile*, *Ixerba brexioides*, *Laurelia novae-zelandiae*, *Litsea calicaris*, *Metrosideros excelsa*, *Syzygium maire*, *Alectryon excelsus* and *Vitex lucens*. These warm-temperate forests tend to have a low diversity of terrestrial bryophyte cover; relatively dry-tolerant mosses such as *Leucobryum candidum* dominate, and terrestrial liverworts are usually restricted to damp sites particularly near streams, or on leaf-litter-free sites such as tree fern bases. Rotting logs are less of a feature of the forest floor than in the cool-temperate zone and often are dominated by mosses. The epiphytic liverwort flora is abundant in high-rainfall areas.

Nothofagus occupies extensive mountain areas in the lower and upper montane forest zones of the South Island, but is more limited in its distribution in the North Island due to competition from warm-temperate species and from the smaller extent of higher-elevation land. There are four species: *N. fusca* occupies warmer and more fertile sites, especially on north-facing hillslopes and in frost-free valleys and between ridges; *N. truncata* is found mainly on ridges; *N. menziesii* occurs in cool and sometimes rather infertile sites especially in South Westland and Fiordland; and *N. solandri* is found in similar cool and somewhat infertile but drier sites. *Nothofagus* tends to exclude other canopy-forming species, but two tree species frequently share the canopy with *Nothofagus*: *Griselinia littoralis* and *Weinmannia racemosa*, the latter of which is sometimes a canopy co-dominant, particularly with *N. fusca*. Where *Nothofagus* is absent from montane forests, particularly in Central Westland, the midslopes of Mt. Taranaki and Stewart Island, *Weinmannia racemosa* forms forests with *Metrosideros umbellata* and *Quintinia serrata* with *Libocedrus* emergent. *Nothofagus* forests offer excellent bryophyte habitats because they offer a fairly low canopy, their small leaves do not smother terrestrial habitats with leaf litter, and understory shrubs and ground herbs are often quite sparse. *Weinmannia–Metrosideros* forests, on the other hand, are less favorable for bryophytes, but the large root systems of *Metrosideros* offer protected habitats to a distinctive assemblage of bryophyte species that includes, most notably, several *Zoopsis* species.

INTRODUCTION

Seral forests of *Aristotelia serrata*, *Fuchsia excorticata*, *Hoheria*, *Plagianthus* (all deciduous), and *Carpodetus serratus*, *Melicytus ramiflorus*, *Pseudopanax* spp. and *Schefflera digitata* are common around slips and riverbanks in the lowland and montane zones. Due to their low canopy (ca. 10 m), proximity to streams and deciduousness, these forests provide a good liverwort habitat.

The most common scrub type in New Zealand is formed by *Leptospermum scoparium*, which occurs throughout the country except on the Kermadec Islands. It is a very common and abundant seral vegetation after burning, particularly on wet or organic soils. The taller *Kunzea ericoides* is often seral in similar habitats in lower rainfall areas.

A distinctive type of heathland grading to fern-rushland, termed "pakihi" in the South Island and Stewart Island and "gumlands" in Northland and Coromandel, forms on flat terraces or low-angled hills after removal of forest. Gumlands and pakihi differ in floristic composition, e.g., the species composition involving *Dracophyllum* and *Baumea*, but their soils, vegetation structure and history are broadly the same (Wardle, 1991, p. 201). The soils of these heathlands are gleyed and podzolized, with resulting perched water tables and low fertility. These communities are composed of varying and changing proportions of *Leptospermum scoparium*, *Gahnia rigida*, *Baumea* spp., *Empodisma minus*, *Gleichenia dicarpa* and *G. microphylla*.

Gumlands and pakihi occur in Northland, Coromandel, Western Nelson, Westland and Stewart Island, replacing mainly *Agathis australis* and *Dacrydium cupressinum* forests where these were logged and burned. Such communities can persist for decades, depending on drainage, soil fertility and frequency of fire, until the *Leptospermum* eventually forms a closed scrub canopy that forms shelter for seedlings of tree species. This vegetation type appears to have been created mostly by logging and burning of conifer forests, but pollen analysis of Northland gumlands indicates the vegetation type was present 16,000 years ago as a result of natural fires (Wardle, 1991). The extensive areas of these induced heathlands created in the twentieth century are now diminishing due to fire restrictions. *Goebelobryum unguiculatum*, *Lethocolea pansa* and *Neogrollea notabilis* are confined to this habitat in New Zealand, while *Kurzia compacta*, *K. helophila*, *Riccardia multicorpora*, *R. pusilla*, *Telaranea herzogii* and *T. quinquespina* occur in these habitats along with the distinctive mosses *Pleurophascum ovalifolium* and *Pulchrinodus inflatus*.

A distinctive liverwort community exists in what has been termed the "Murihiku alliance" (C. Meurk, pers. comm., 2005) of conifer scrub, particularly *Lepidothamnus intermedius* and *Halocarpus biformis*, mixed with low *Nothofagus solandri* and *Metrosideros umbellata.* Scrub of this type may have naturally formed a mosaic of scrub and pakihi, and most of it has been burned to some degree. Where burned, it has formed open fern-rushlands (pakihi). This vegetation occurs in southern Stewart Island, the highest station occurs at Waitutu Forest, Cascade Plateau, and small pockets remain throughout Westland, Stockton and Denniston plateaus, Gunnar Downs and in small areas in the North Island at treeline on Mt. Ruapehu and Mt. Moehau. This scrub is particularly rich in liverworts because the canopy is low, the soils are infertile (and therefore competition from vascular plants is low) and also the usual occurrence of peat over granite holds moisture well; the scrub is found only under high rainfall. Liverwort species occurring in this scrub are *Acromastigum brachyphyllum*, *Blepharidophyllum vertebrale*, *Clandarium xiphophyllum*, *Eotrichocolea polyacantha*, *Isolembidium cucullatum*, *Megalembidium insulanum*, *Pseudolophocolea denticulata*, *Saccogynidium decurvum*, *Telaranea inaequalis*, *Zoopsis bicruris* and epiphytes *Goebeliella cornigera*, *Heteroscyphus menziesii*, *Jubulopsis novae-zelandiae* and *Schistochila pseudociliata.* The combination of *Acromastigum cavifolium*, *Archeophylla schusteri*, *Brevianthus flavus*, *Herzogianthus sanguineus* and *Leptoscyphus australis* in this scrub type is distinctive.

Nothofagus solandri and *N. menziesii* commonly form the upper limit of forest and may form scrub 2–3 m high near treeline on exposed ridges. However, penalpine scrub composed mainly of *Olearia colensoi*, *O. ilicifolia*, *Brachyglottis rotundifolia*, *Dracophyllum longifolium* and *D. rosmarinifolium* commonly occurs above treeline.

Grasslands

Grasslands occur naturally in the penalpine and alpine zone, and in river valleys where forests are excluded by severe winter frosts. In such river valleys, and presently on extensive valleys and hillslopes formerly occupied by forest, *Festuca novae-zelandiae*, *F. matthewsii*, and in damper and more fertile soils, *Poa cita* form what are often termed "short tussocklands" to distinguish them from the tall *Chionochloa* tussocklands of higher elevations. These grasslands now are densely populated by adventive grasses such as *Anthoxanthum odoratum* and *Agrostis capillaris* and offer a bryophyte habitat only where soils are too thin for grasses to grow.

Chionochloa pallens and *C. flavescens* are the main species in the penalpine tussock zone in western provinces of the South Island and form large tussocks typically 0.5–1.0 m high. These are a good habitat for bryophytes where they grade into *Celmisia* herbfield, particularly on shaded south-facing slopes and around rock outcrops. *Blepharidophyllum vertebrale*, *Clandarium xiphophyllum*, *Gackstroemia alpina*, *Heteroscyphus billardierei*, *Lepidogyna hodgsoniae*, *Paraschistochila conchophylla*, *Riccardia pennata*, *Schistochila monticola* and the hornwort *Megaceros giganteus* are characteristic of this habitat, and *Eotrichocolea polyacantha*, *Phyllothallia nivicola* and *Riccardia pseudodendroceros* have been found in such sites. *Chionochloa macra* and *C. rigida* replace *C. pallens* in equivalent habitats east of the Main Divide, but the habitats are too dry for liverworts except around streams and seepages. *Chionochloa crassiuscula* and *C. oreophila* occur at higher altitudes in the alpine zone and are often mixed with *Poa colensoi* and *Celmisia*-dominated herbfields. *Chionochloa rubra* tussocklands occur above treeline in the North Island and northern South Island, particularly on low-angled and infertile organic soils, but are more often associated with wetlands on peaty soils below treeline. In the northern half of the South Island *C. australis* forms dense mats that tend to exclude bryophytes.

Wetlands

The many wetland types in New Zealand for the most part lack any significant diversity of bryophytes. Estuarine wetlands lack bryophytes because these plants are not salt-tolerant. In the large gravel riverbeds species of the moss *Racomitrium* may dominate, but the habitat is too dry and exposed to support a liverwort flora. Two broad classes of freshwater wetlands may be distinguished by their fertility and water flow: swamp and bogs.

Swamps, usually in the lowland zone, are dominated by *Typha orientalis*, *Phormium tenax* and the large sedge *Carex secta*; other *Carex* species such as *C. sinclairii* and *C. gaudichaudiana* can form extensive sedgelands. Floating plants are *Azolla*, *Callitriche*, *Lemna*, *Potamageton* and the liverwort *Ricciocarpos natans*. Swamps usually are not rich in bryophytes, and the liverworts to be found in swamps are usually rather common unspecialized species, e.g., *Marchantia foliacea* and *Chiloscyphus* species.

Bogs, by contrast, are a habitat for a diverse set of liverworts that require constant moisture but tolerate high light levels. Most bogs occur in the penalpine and lower alpine zone in the

North and South islands but reach sea level on Stewart Island and the subantarctic islands. Two cushion-forming species, *Oreobolus pectinatus* and *Donatia novae-zelandiae*, commonly form much of the cover, and the mosses *Sphagnum cristatum* and *S. falcatulum* are present in well-inundated areas. *Carpha alpina*, *Centrolepis ciliata*, *Chionochloa rubra*, *Halocarpus bidwillii* and *L. laxifolius* are also common, and bogs often grade into low podocarp scrub. Liverwort genera that have their main occurrence in bogs are *Austrofossombronia, Calypogeia*, *Cephalozia*, *Cephaloziella*, *Goebelobryum*, *Metahygrobiella* and *Pseudocephalozia*. Certain species of *Acromastigum*, *Allisoniella*, *Kurzia*, *Telaranea* and *Riccardia* also have their main occurence in bogs.

Liverworts in flushes in the penalpine and alpine zones experience similar conditions to bogs but nutrient levels may be higher. *Austrofossombronia*, *Cryptochila*, *Marchantia*, *Marsupella* and *Scapania* are found in flushes, in addition to many of the genera and species of bogs listed above.

Aquatic liverworts occur mostly on rock, usually in very small streams, beside waterfalls and cascades, or are found on rock surfaces that are covered by a thin film of water seepage, as abrasion of leaves by sediment limits bryophyte growth in most large streams and rivers. Species and genera that have their main occurrence in this habitat are *Allisoniella recurva*, *Cephalomitrion aterrimum*, *Cryptochila grandiflora*, *Eoisotachis stephanii*, *Hepatostolonophora rotata*, *H. paucistipula*, *Isophyllaria attenuata*, *Monoclea forsteri*, *Pachyglossa tenacifolia*, *Schistochila kirkiana*, *S. nitidissima*, *S. pellucida* and species of *Aneura*, *Lejeunea*, *Riccardia* and *Plagiochila.*

Ricciocarpos natans and *Riccia fluitans*, both of cosmopolitan distribution, are the only free-floating aquatic species, but also can be found on mud in lowland swamps after water levels drop. Both appear to be much less common now than formerly.

Sparsely vegetated alpine habitats

In the alpine zone, sparsely vegetated surfaces provide a habitat for bryophytes: rock surfaces because the soil is too thin for vascular plants, and soil pockets and overhangs because they are protected from rain but receive cloud moisture from fog. A very distinctive bryophyte flora found on rock and thin mineral soils in exposed sites has *Acrolophozia pectinata*, *Andreaea acuminata*, *A. acutifolia*, *Andrewsianthus cuspidatus*, *Diplophyllum domesticum* var. *icari*, *Gymnomitrion cuspidatum*, *Herzogobryum teres*, *Nothogymnomitrion erosum*, *Solenostoma rufiflorum* and *S. totipapillosum*. *Dracophyllum pronum* is often associated with such sites. Conditions are less extreme on rock sites with water seepage (including snow melt) but otherwise free of vascular plants because of a lack of soil; *Allisoniella*, *Cephalomitrion*, *Cephalozia*, *Hepatostolonophora*, *Solenostoma inundatum*, *Temnoma* and *Triandrophyllum subtrifidum* are characteristic.

8. Principal substrates of New Zealand liverworts

The forest floor

The litter of some of the most abundant New Zealand trees, especially *Nothofagus solandri* and *N. menziesii*, but also all of the native conifers, is small enough that bryophytes growing

on slightly uneven sites on the forest floor are able to survive inundation by the steady but light rain of leaf litter, undoubtedly assisted in this by the almost complete lack of deciduous tree species in New Zealand. *Lepidoziaceae* genera (*Lepidozia*, *Bazzania*, *Megalembidium*, *Telaranea*) are very successful in this situation, but other genera such as *Trichocolea*, *Leiomitra*, *Lepidogyna*, *Chiloscyphus*, *Heteroscyphus*, *Plagiochila*, *Schistochila* and *Hymenophyton* do equally well in these sites and are competitive against mosses such as *Dicranoloma* which specialize in this habitat. However, it is noticeable that in the northern half of the North Island, where larger-leaved tree species such as *Dysoxylum*, *Elaeocarpus* and *Beilschmiedia* dominate, terrestrial species are confined to sloping sites where leaf litter is unable to accumulate, or near streams where flooding regularly removes leaf litter. Where the ground is more uneven, particularly in the cooler southern forests, other less competitive genera, such as *Acromastigum*, *Anastrophyllum*, *Chandonanthus*, *Gackstroemia* and *Lepidolaena*, find a place on the forest floor.

Rotting logs and stumps are prime habitat for a diverse range of terrestrial liverworts because they shed leaf litter from their sloping surfaces, water is held by the decaying wood, and in the case of large logs they are comparatively well lit by being raised from the forest floor. Later in log or stump succession, bryophyte mats and the tight, interlaced root bases of hymenophylls are conducive to water retention. Rates of decay of logs and stumps are slow in the cool-temperate zone, and consequently they cover significant parts of the forest floor. *Lophocoleaceae* genera such as *Chiloscyphus* and *Heteroscyphus* excel in this habitat, as do *Lepidoziaceae* genera. In addition to all the forest floor genera listed above, *Jamesoniella*, *Marsupidium*, *Plagiochilion*, *Riccardia*, *Schistochila*, *Tylimanthus* and *Wettsteinia* have their main habitat on rotting logs.

Soil and humus under tree roots and in tree-root caves provide a habitat protected from the litter rain, but such sites are difficult because of their lack of moisture and dim light conditions. *Zoopsis* is extremely well adapted to these conditions by virtue of the large lens-like stem cortex cells that focus light on chloroplasts on the back walls of the cells and the reduced leaves that limit water loss. Other species adapted to these conditions are *Bazzania nitida*, *Psiloclada clandestina* and *Zoopsidella caledonica*.

Cliff faces, boulder faces, overhangs, stream banks and road and track cuttings within the forested environment (and at its margins) provide favorable environments for liverworts. Such sloping or overhanging sites are free of litter, are often well-lit, and often have water seepage from above or receive direct rainfall. The majority of terrestrial liverworts in New Zealand are found in such sites, with genera such as *Aneura*, *Balantiopsis*, *Chiloscyphus*, *Cryptochila*, *Drucella*, *Geocalyx*, *Heteroscyphus*, *Isotachis*, *Jackiella*, *Lembidium*, *Metzgeria*, *Pallavicinia*, *Plagiochila*, *Radula*, *Riccardia*, *Saccogynidium*, *Solenostoma*, *Temnoma* and *Triandrophyllum* prominent. Roadside banks in Westland and Fiordland are notable for their complete cover of single species such as *Isotachis lyallii*.

Epiphytes

At the base of trees there is no sharp distinction between epiphytes and terrestrial liverworts as soil accumulates and the surfaces are sloping and consequently leaf-litter free. Genera of *Lepidoziaceae* and *Lophocoleaceae* predominate. In Westland, because the humidity above ground level is consistently high, the distinction between terrestrial and epiphytic species is blurred and terrestrial species grow on sloping tree trunk bases up to about 2 m, e.g., *Bazzania adnexa* and *Schistochila nobilis*.

INTRODUCTION

The epiphytes of tree trunks and tree branches can be rather arbitrarily divided into two groups, firstly those of upper montane forests where the canopy is low, light levels are high and strong drying winds at times occur. Species and genera typical of this habitat are *Acrobolbus concinnus*, *Chandonanthus squarrosus*, *Goebeliella cornigera*, *Herbertus oldfieldianus*, *Heteroscyphus menziesii*, *Jamesoniella kirkii*, *Lepicolea attenuata*, *L. scolopendra*, *Paraschistochila tuloides*, *Pseudomarsupidium piliferum*, and species of *Lepidolaena* and *Frullania.* These species for the most part exhibit some adaptations to a more rigorous habitat, e.g., strongly collenchymatous leaf cells, thick-walled stem cells and frequent presence of secondary pigments.

Secondly, epiphytes of lowland and montane forests with a high canopy experience lower light levels (except on forest margins), but the habitat is more constantly moist. Here, typically epiphytic *Plagiochilaceae* species are present, such as *Acrochila biserialis*, *Plagiochila annotina*, *P. circinalis*, *P. deltoidea*, *P. fasciculata*, *P. incurvicolla*, *P. obscura*, *P. radiculosa*, *P. stephensoniana*, *P. strombifolia* and *Plagiochilion conjugatum.* Also typical are *Archilejeunea olivacea*, *Dendromastigophora flagellifera*, *Harpalejeunea latitans*, *Lejeunea flava*, *Mastigolejeunea anguiformis*, *Metzgeria furcata*, *Porella elegantula*, *Radula* spp., and more occasionally, *Bazzania nova*, *B. hochstetteri*, *Chiloscyphus muricatus* and *Heteroscyphus cymbaliferus*.

The bryophyte flora of high tree canopies has not been studied; it is dominated by dry-tolerant epiphytic mosses such as *Papillaria flavolimbata*, *Macromitrium* spp., and the three *Dicnemon* species (*D. calycinum*, *D. dixonianum* and *D. semicryptum*). However, some liverwort species found in this habitat in Westland lowland forest canopies and at times elsewhere are *Acrobolbus concinnus*, *Bazzania nova*, *Chandonanthus squarrosus*, *Cuspidatula monodon*, *Drepanolejeunea aucklandica*, *Diplasiolejeunea plicatiloba*, *Lepidolaena palpebrifolia*, *L. taylorii*, *Paraschistochila tuloides*, *Plagiochila deltoidea*, *Plagiochilion conjugatum* and *Pseudomarsupidium piliferum.*

A distinctive epiphytic twig bryophyte flora is present in New Zealand, particularly at the margins of lowland forests. *Coprosma* species have the richest twig bryophyte flora, particularly *C. propinqua*, *C. rhamnoides*, *C. rotundifolia* and *C. tayloriae*. *Austrolejeunea olgae*, *Austrometzgeria saccata*, *Cololejeunea* spp., *Colura pulcherrima* var. *bartlettii*, *Dinckleria pleurata, Diplasiolejeunea plicatiloba*, *Drepanolejeunea aucklandica*, *Harpalejeunea latitans*, *Lejeunea* species, *Lopholejeunea colensoi*, *Metzgeria furcata*, *M. scobina*, *M. flavovirens* and *Siphonolejeunea nudipes* are common twig epiphytes of damp forest margins, and often are found with mosses such as *Crosbya straminea*, *Ephemeropsis trentepohlioides* and *Tetraphidopsis pusillus*. In drier, exposed habitats *Frullania*, and to a lesser extent *Radula*, are the only liverwort genera that compete with the more dry-tolerant mosses, while in exposed but high-rainfall situations *Jubulopsis novae-zelandiae* and *Nephelolejeunea conchophylla* are rare endemics, found mainly on twigs of *Leptospermum* and *Metrosideros* (both *Myrtaceae*).

Variation in the epiphytic liverwort flora between host species is quite noticeable, but insufficient collections recording the host have been made to quantify the differences. For example, *Melicytus ramiflorus* and *Pseudowintera colorata* and some *Coprosma* species are favored hosts, particularly for twig epiphytes, as well as *Metrosideros*, both vine and tree species, and other *Myrtaceae* genera such as *Kunzea*, *Leptospermum* and *Neomyrtus*, in addition to all of the native conifer species despite their peeling or flaking bark. However, a wide variety of tree species are also recorded as hosts.

Tree ferns (*Cyathea* and *Dicksonia*) are a conspicuous element of the understory in New Zealand forests of all types, particularly in canopy light gaps. *Symphyogyna subsimplex* is the only liverwort species confined to tree fern caudices; *Bazzania tayloriana* and *Chiloscyphus helmsianus* are mainly found on tree fern caudices, especially on their wide bases, and *Baz-*

zania nova, *Podomitrium phyllanthus*, *Psiloclada clandestina*, *Schistochila pluriciliata* and *Zoopsis argentea* are sometimes found in this habitat.

Epiphylls

Epiphyllous taxa occur only in high-humidity environments, especially on leaves or fern fronds close to the ground near streams. A number of biotic and abiotic factors impact the epiphyllous condition, such as high atmospheric humidity, leaf longevity and light (see Corley et al., 1993; Gradstein and Pócs, 1989; Richards, 1984; von Konrat and Braggins, 1999a). For a discussion of life history strategies and epiphyllous liverworts see Longton and Schuster (1983) and Schuster (1991). Among the ferns and fern allies, the main hosts of liverwort epiphylls are of the genus *Blechnum*, such as *B. nigrum* and *B. colensoi* (both ferns of very damp shady environments), *B. chambersii*, *B. filiforme*, *B. discolor*, *B. minus*, *B. novae-zelandiae*, *B. procerum*, *Hymenophyllum* and *Trichomanes* species, *Polystichum vestitum*, and rarely *Microsorum*, *Lycopodium* and *Tmesipteris*. *Pseudowintera colorata* is the most notable of the flowering plant hosts for epiphylls and may have complete liverwort cover on some leaves, and among the strap-leaved monocots, the most notable is *Freycinetia baueriana*. Epiphylls have been recorded on the following tree species: *Alectryon excelsus*, *Ascarina lucida*, *Beilschmiedia tawa*, *Knightia excelsa*, *Laurelia novae-zelandiae*, *Nothofagus menziesii* and the palm *Rhopalostylis sapida*. These fern and flowering plant hosts, with the exception of *Nothofagus*, are also the main hosts of foliicolous lichens. This suggests that a lack of tannins and a less waxy leaf surface may better enable spores and plants to adhere and become established, and may be partial explanations for their frequency as hosts.

Most genera of *Lejeuneaceae* can be found as epiphylls, but some species of *Frullania* (see von Konrat and Braggins, 1999a), *Lepidolaena*, *Metzgeria*, *Riccardia* and *Telaranea* can be epiphyllous. *Kymatolejeunea bartlettii* and *Nephelolejeunea papillosa* have only been found among the leaves of the large moss *Dendroligotrichum dendroides*, which is also commonly a host for *Colura saccophylla* and *C. pulcherrima* (but these two species also occur as twig epiphytes). *Echinolejeunea papillata* is found almost exclusively on fern fronds (*Blechnum*, *Hymenophyllum*, *Trichomanes*, *Grammitis* and *Polystichum*).

Cololejeunea hodgsoniae is often found on mosses and larger liverworts such as *Plagiochila stephensoniana* on lowland forest stream margins, and *Cheilolejeunea campbelliensis* is most commonly found on mosses and liverworts such as *Breutelia elongata* and *Clandarium xiphophyllum* in penalpine scrub.

9. Distribution and range of liverwort species within New Zealand

Liverworts appear to be somewhat less climatically limited in their range than the vascular plants of New Zealand. Only one liverwort species spans the range between the Kermadec Islands and Campbell Island: *Marchantia berteroana. Marchantia foliacea* ranges from the Kermadec to Auckland islands. However, a large number of liverwort species are present from the subantarctic islands to Northland; a greater proportion of the liverwort flora has this wide range than does the vascular flora. A number of species of *Jungermanniideae* have a broad range in New Zealand, notably *Chandonanthus squarrosus*, *Cuspidatula monodon*, *Jamesoniella colorata*, *J. kirkii*, *J. tasmanica* (all span Auckland Islands to Northland), but

other very wide-ranging species are *Bazzania adnexa*, *B. involuta*, *Chiloscyphus bispinosus*, *Drepanolejeunea aucklandica*, *Harpalejeunea latitans*, *Heteroscyphus coalitus*, *Hymenophyton flabellatum*, *H. leptopodum*, *Lamellocolea granditexta*, *Lejeunea primordialis*, *Lembidium nutans*, *Lepidolaena taylorii*, *L. clavigera*, *Lepidozia concinna*, *L. laevifolia*, *L. microphylla*, *Lopholejeunea colensoi*, *Metzgeria furcata*, *Monoclea forsteri*, *Pallavicinia xiphoides*, *Paraschistochila pinnatifolia*, *P. tuloides*, *Plagiochila gigantea*, *P. intertexta*, *P. radiculosa*, *Podomitrium phyllanthus*, *Porella elegantula*, *Psiloclada clandestina*, *Radula grandis*, *R. marginata*, *R. physoloba*, *R. silvosa*, *R. uvifera*, *Riccardia aequicellularis*, *R. cochleata*, *R. crassa*, *Saccogynidium australe*, *Tylimanthus tenellus* and *Zoopsis argentea.* Fewer than average of these species (29%) are endemic to New Zealand, as might be expected, but *Monoclea forsteri* and *Lembidium nutans* (Campbell Island to Northland) are notable exceptions; both are very common and widespread New Zealand endemics. Many liverwort species have more restricted distributions, and in general two distribution types are the most common. First are southern species that have their northern limit in the South Island or, more commonly, in the North Island mountains. The second, less common distribution type consists of northern species that have their southern limit in the North Island or in northern or western lowlands of the South Island.

Cool-temperate species that are found almost exclusively in the South Island and further south and have a northern limit that may be limited by climate are *Acrobolbus cinerascens*, *Acromastigum mooreanum*, *A. verticale*, *Archeophylla schusteri*, *Castanoclobos julaceus*, *Clandarium xiphophyllum*, *Cryptochila acinacifolia*, *Eoisotachis stephanii*, *Eotrichocolea polyacantha*, *Isolembidium cucullatum*, *Isophyllaria attenuata*, *Jubulopsis novae-zelandiae*, *Kurzia tenax*, *Lepidozia ulothrix*, *Megalembidium insulanum*, *Metzgeria rigida*, *Pachyglossa tenacifolia*, *Radula ratkowskiana*, *R. tasmanica*, *Schistochila lehmanniana*, *Telaranea tetradactyla*, *T. pulcherrima* and *T. tuberifera.* Most of these species can be found near sea level in the south of New Zealand but are confined to the penalpine zone at their northern limit, which is in the Ruahine and Tararua ranges for some (e.g., *Diplophyllum domesticum* var. *icari*, *Lepidozia ulothrix*, *Metahygrobiella drucei*, *Neohodgsonia mirabilis*, *Pachyschistochila parvistipula*, *Paraschistochila conchophylla* and *Phyllothallia nivicola*), at Mt. Taranaki for others (e.g., *Cheilolejeunea campbelliensis*, *Clasmatocolea strongylophylla*, *Hygrolembidium australe*, *Isotachis intortifolia*, *Lepidolaena reticulata*, *Plagiochila ramosissima*, *P. strombifolia*, *Telaranea quadriseta*) or at Mt. Ruapehu (e.g., *Archeophylla schusteri*, *Cephalomitrion aterrimum*, *Cryptochila pseudocclusa*, *Eotrichocolea polyacantha*, *Herzogobryum teres*, *Isophyllaria attenuata*, *Lepidozia ornata*, *Nothogymnomitrion erosum*, *Pseudolophocolea denticulata* and *Telaranea trilobata*). Some southern species have their northern limit in the middle of the South Island, particularly in the mountains of Western Nelson EP. Examples are *Telaranea meridiana*, *Wettsteinia schusteriana* (southern end of Paparoa Range) and *Cryptochila acinacifolia* (Mt. Euclid in the central Paparoa Range).

Warm-temperate species that are mainly found in the North Island but can be found in Nelson and lowland parts of Westland are *Acrolejeunea allisonii*, *A. mollis*, *Asterella australis*, *Bazzania tayloriana*, *Chaetophyllopsis whiteleggei*, *Chiloscyphus echinellus*, *Cololejeunea hodgsoniae*, *C. pulchella*, *Drucella integristipula*, *Geocalyx caledonicus*, *Jackiella curvata*, *Marchantia macropora*, *Mastigolejeunea anguiformis*, *Nephelolejeunea hamata*, *Paracromastigum furcifolium*, *Plagiochilion prolifer*, *Radula papulosa*, *Ricciocarpos natans*, *Telaranea gibbsiana* and *Trichocolea hatcheri*.

Many tree species of northern New Zealand have their southern limit between Kawhia Harbour and East Cape, e.g., *Agathis australis*. Some liverworts seem similarly limited and include a subtropical element composed of *Cololejeunea cardiocarpa*, *Dumortiera hirsuta*, *Harpalejeunea filicuspis* and *Leptolejeunea elliptica* but also the endemics *Frullania wairua*,

Telaranea granulata, *T. perfragilis* and *Stenolejeunea acuminata*, and the epiphytic hornwort *Dendroceros granulatus*. Von Konrat et al. (2006a) pointed out that the New Zealand distribution of *Frullania chevalieri*, a species otherwise known from New Caledonia, appears to be somewhat correlated with that of *Agathis australis* forest, and that it would be of interest to determine whether the southern range of *F. chevalieri* is the same as that forest type.

The following liverwort species show a disjunction between Northland EP (especially Waipoua) or Auckland EP (especially Coromandel Peninsula, Great Barrier or Little Barrier islands) and Westland–Fiordland–Rakiura EPs: *Acrochila biserialis*, *Acromastigum cavifolium*, *A. marginatum*, *Brevianthus flavus*, *Goebelobryum unguiculatum*, *Lembidium longifolium*, *Lepidozia setigera*, *Mnioloma novae-zelandiae*, *Zoopsis ceratophylla* and *Z. nitida.* The moss *Pulchrinodus inflatus* shows the same disjunction, as do a few vascular species such as *Metrosideros parkinsonii*. The reasons for this disjunction seem to be in part climatic and in part a disjunction in habitat such as pakihi/gumlands.

A number of alpine species are present in the South Island mountains but absent from Stewart Island or the subantarctic islands: *Acrolophozia pectinata*, *Anthelia juratzkana*, *Austrolophozia paradoxa*, *Bragginsella anomala*, *Diplophyllum gemmiparum*, *D. verrucosum*, *Gymnomitrion cuspidatum*, *G. strictum*, *Herzogobryum filiforme*, *Heteroscyphus mononuculus*, *Isotachis intortifolia*, *I. olivacea*, *I. plicata*, *Marsupella sparsifolia*, *M. sprucei*, *Pachyschistochila altissima*, *P. berggrenii*, *P. childii*, *P. nivicola*, *P. parvistipula*, *P. succulenta*, *P. trispiralis*, *P. virescens*, *Ptilidium ciliare*, *Radula sainsburiana*, *Scapania nemorosa* and *S. undulata.*

Some of these species (*Anthelia juratzkana*, *Ptilidium ciliare*, both species of *Scapania* and both species of *Marsupella*) are bipolar in range; they are found in the Northern Hemisphere in temperate to arctic conditions, and are pre-adapted to the alpine zone. There is a lack of obvious radiation in the alpine zone liverwort flora, due no doubt to the recency of the Southern Alps, and speciation seems to have been notably slower than in vascular plants, where major radiations have occurred (e.g., *Aciphylla*, *Celmisia*, *Gentianella* and *Ranunculus*). Only in *Pachyschistochila* can such a radiation be seen.

There are no known liverwort disjunctions corresponding to the beech gap in Westland between the Taramakau and Karangarua rivers.

Some species are known from a single region; examples are *Cololejeunea falcidentata*, *Frullania wairua* and *Schistochila nitidissima* of Northland, *Schistochila pellucida* of the Volcanic Plateau, and *Pachyschistochila papillifera* of the Ruahine Range. The complete range of such local endemics is not known and is likely to have been reduced by habitat loss. A much more comprehensive knowledge of the liverwort flora is needed to understand patterns of local endemism.

10. Rarity and conservation

New Zealand has its own threatened species classification (Molloy et al., 2002) developed by the Department of Conservation, which has the role of advocacy and management of threatened species. The classification is a two-tiered system:

Extinct: no reasonable doubt exists after repeated survey that the last individual has died. No New Zealand liverworts are in this category.

Acutely threatened (taxa that face a high risk of extinction in the wild):
Nationally critical: very small population or a very high predicted decline.
Nationally endangered: small population and moderate to high, recent or predicted decline.
Nationally vulnerable: small to moderate population and moderate decline.
Chronically threatened (taxa that face extinction but are buffered by a large total population or slow rate of decline):
Serious decline: moderate to large population and moderate to large decline.
Gradual decline: moderate to large population and small to moderate decline.
At risk (not presently facing a risk of extinction, but could be if new threats depleted their populations):
Sparse: naturally or unnaturally rare but not restricted to a small geographical area.
Range restricted: naturally or unnaturally rare, restricted to a small geographic area, a specific habitat or substrate.
Data deficient: information is too poor to assign them to one of the categories above.

The Department of Conservation maintains threatened species lists of most groups of organisms, including bryophytes. Listed species have no statutory protection. As of 2005 it contained 157 liverwort species, 41 of which were in the nationally critical category (Glenny and Fife, 2005). The composition of the list is not yet stable because of insufficient knowledge of distributions of the rarer species, the active state of New Zealand liverwort taxonomy and the recency of the list's compilation.

11. Guidance to users of the flora

Geographical scope

The geographical coverage of the flora includes the three main islands of New Zealand, i.e., Stewart Island, South Island and North Island. It includes what are often termed the "outlying islands": Campbell, Auckland, Antipodes, Bounty, Snares, Chatham and Kermadec Islands, as well as all the "offshore islands" such as Three Kings Islands, Great Barrier Island, Little Barrier Island, Solander Island, Muttonbird Islands and Whenua Hou (Codfish Island) (Map 1). The flora excludes Macquarie Island, which although considered part of the New Zealand region, is politically part of Australia and is included in the *Flora of Australia*.

Intent of the flora

The intent of the flora is to treat all New Zealand liverworts and hornworts in a manner that is useful to a broad audience, e.g., to professionals, students, amateurs and conservation organizations. The treatment of each species includes a section on synonymy, a description of the plant, statements of world distribution, with more detailed comments of range within New Zealand, as well as a discussion of ecology. For ease in identification, full or nearly full descriptions are provided. Many groups have been subjected to study for the first time, and the flora therefore contains much information that is presented here for the first time. Likewise, many taxa have gametangia, sporophyte and oil-body detail described and often illustrated for the first time. Comments on extra-territorial taxa are typically included in the relevant taxonomic category, i.e., as part of discussions of families or genera.

INTRODUCTION

Classification

The sequence of orders and families presented in this flora is based for the most part on the classifications of Schuster (1979a, 1984e, 2000a, 2002a). However, moderate to considerable variants are made in this treatment, e.g., the recognition of *Megalembidium* in its own subfamily juxtaposed to subfam. *Lembidioideae*, the placement of *Neogrollea* in its own suborder and the position of *Trichotemnomaceae*.

Within genera, the order in which species are treated follows a sequence from what we consider to be "most generalized" to what is considered to be "most derived."

A number of laboratories have been working on molecular phylogenetic studies of liverworts and hornworts in the past five years. The first molecular surveys of large numbers of families and genera reported results quite different from traditional classification schemes, but more careful and complete surveys at the same level are now reporting phylogenies that are very similar to traditional classifications. This gives confidence that traditional classifications are probably basically correct. It is a little too soon to modify traditional classifications with the results of molecular studies, and we have opted to maintain a more traditional approach.

Author citations follow the International Plant Names Index (IPNI, 2006, http://www.ipni.org/index.html) but G. L. Merrill is cited as "Merrill" instead of G.L.Sm. Journal citations follow the abbreviations in Botanico-Periodicum-Huntianum (B-P-H). New synonymy is noted by the designation "*syn. nov.*"

Taxon names at all ranks have been italicized except where they appear as headings and accepted names in the Index. This is in accordance with the style adopted in the *International Code of Botanical Nomenclature* and recommended in the preface (McNeill et al., 2006, p. viii).

Types

Nomenclature and literature citations are included for each species, including all homotypic synonyms; this is followed by citation of the type. We have not used the term "holotype" for species described in the earlier literature, e.g., of the many species originally described by Hooker, Taylor, Colenso or Stephani. These individuals worked in a period prior to the establishment of the current type method, and, in our view, the terms holotype and isotype should not be applied to the original material on which their taxa were based. It should be emphasized that the terms holotype, lectotype, syntype and neotype, etc., were used in the *International Code* for the first time in 1952 (see Lanjouw, 1952). We have opted to utilize the more general term "type" for taxa in the earlier literature (see also Engel, 1978). If an author has merely said "type" when describing a species after 1952, we have used the term "holotype" if the location and identity of the type is clearly given. Herbarium citation is included only in those cases where we have examined a type; in cases where we have not studied the type, no herbarium designation is provided. Lectotypification is not attempted in the flora, a few instances excepted.

Materials used

The senior author has consulted specimens from numerous herbaria, the most significant being BM, CHR, FH, G, JE, NY, S and W. The junior author has examined all specimens at CHR and WELT except for species where large numbers precluded study of all of them.

INTRODUCTION

Species descriptions are nearly all based solely on New Zealand material. Measurements of leaf cells are based on multiple measurements each comprised of a series of cells (ca. 2–5) per measurement rather than a measurement of length and width of an individual cell.

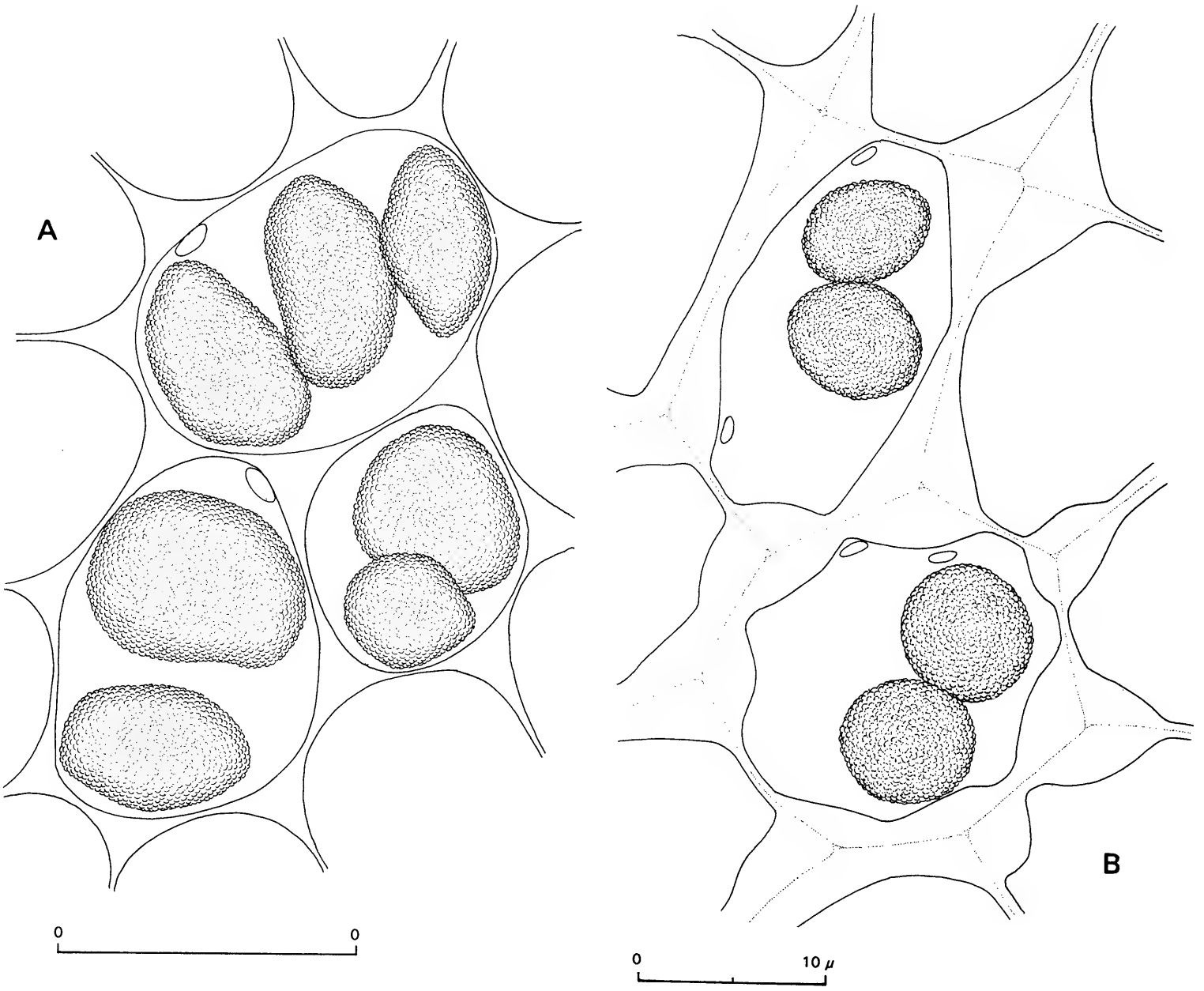
Dimensions are all given as width × length.

Oil-bodies

Oil-bodies are illustrated and data included for at least one species of each genus. Oil-bodies were measured and digitally photographed in New Zealand from fresh material collected by Glenny or Engel. Specimens of Glenny collections were then sent in the fresh state to Chicago for preparation of the figures, using the digital photographs as a reference for the fresh state.

We have attempted to categorize oil-body types based upon a number of criteria. In some cases, however, oil-bodies do not clearly and distinctly fit into a category and placement is somewhat subjective. This is particularly the case with boundaries between the "coarsely granular" and "finely papillose" types and between the "coarsely papillose" and "finely botryoidal" types. We have attempted to be consistent in adhering to the category definitions and characteristics outlined below. Examples of oil-body types are included within each category.

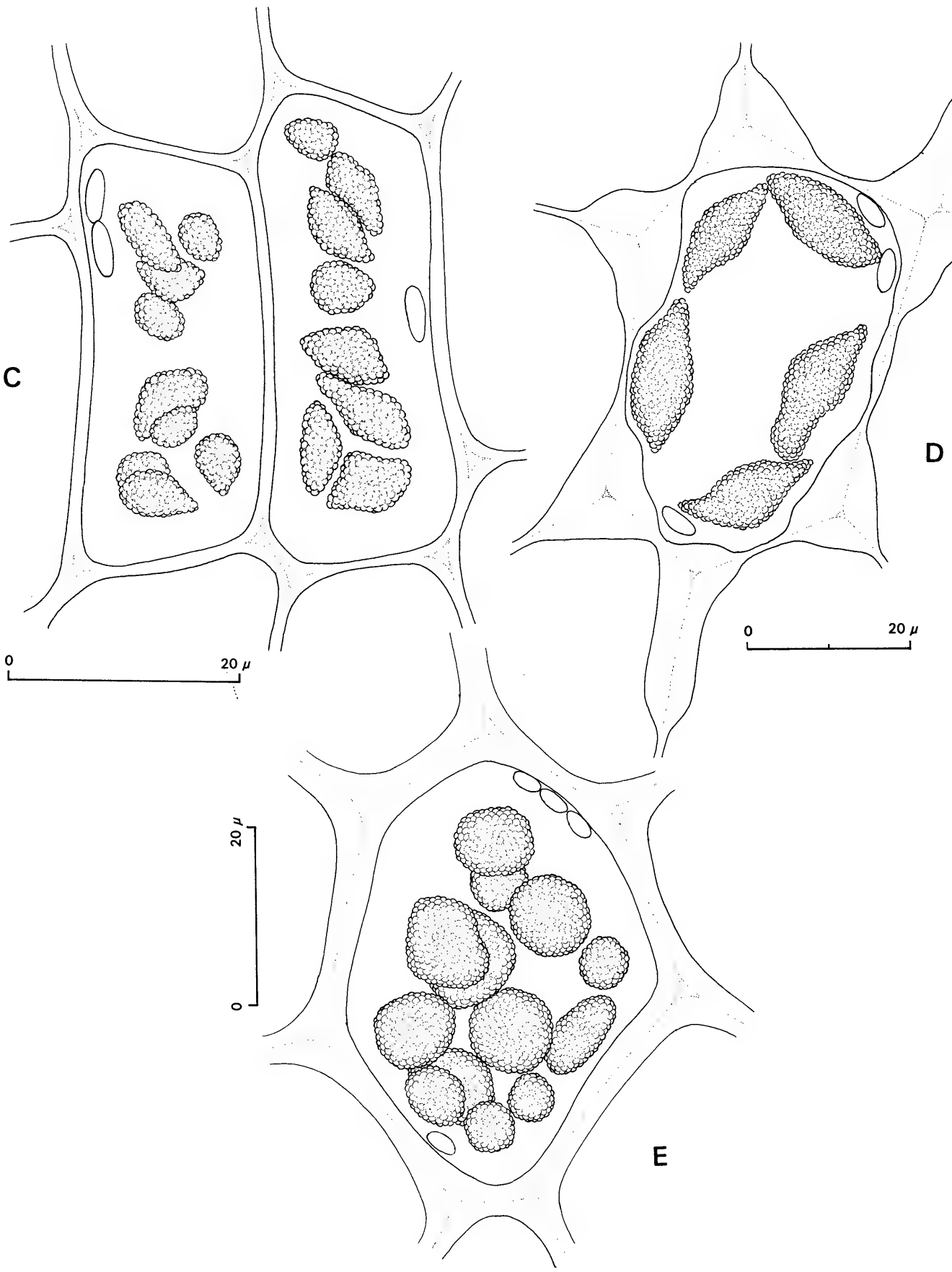
granular: appearing like fine or coarse grains of sand within a membrane; the spherules do not protrude from the relatively firm surrounding membrane; the oil-bodies totally lack

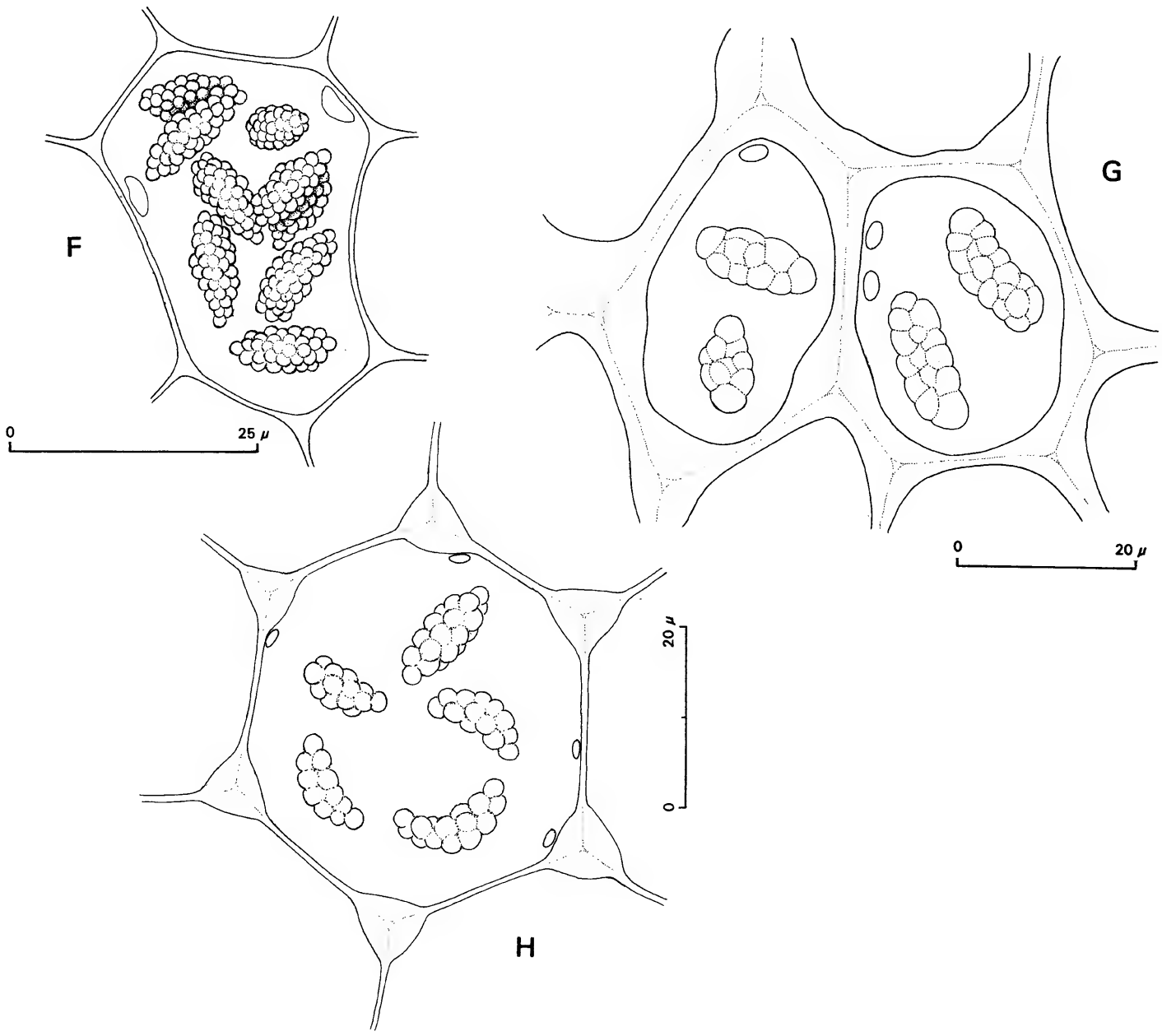


segmentation (see Examples A, *Acrobolbus concinnus* and B, *Archeophylla schusteri*). Breakup occurs by swelling of the entire oil-body followed by a burst of the "grains" through the membrane (or a collapse of the membrane); the "grains" are then free within the cytoplasm (i.e., the "grains" or spherules do not coalesce).

papillose: oil-bodies with discrete segmentation between small (finely papillose) to large (coarsely papillose) spherules, the spherules protruding from the membrane, which is uneven in profile (Examples C, *Adelanthus falcatus*; D, *Acrochila biserialis*; and E, *Pseudomarsupidium piliferum*). Breakup is by way of coalescing of globules, which, with age, become increasingly large, and the internal segmentation gradually fewer.

botryoidal: with the characteristics of the "papillose" condition, but the protrusions greater, the globules larger and the segmentation distinct (Examples F, *Mnioloma novae-zealandiae*;

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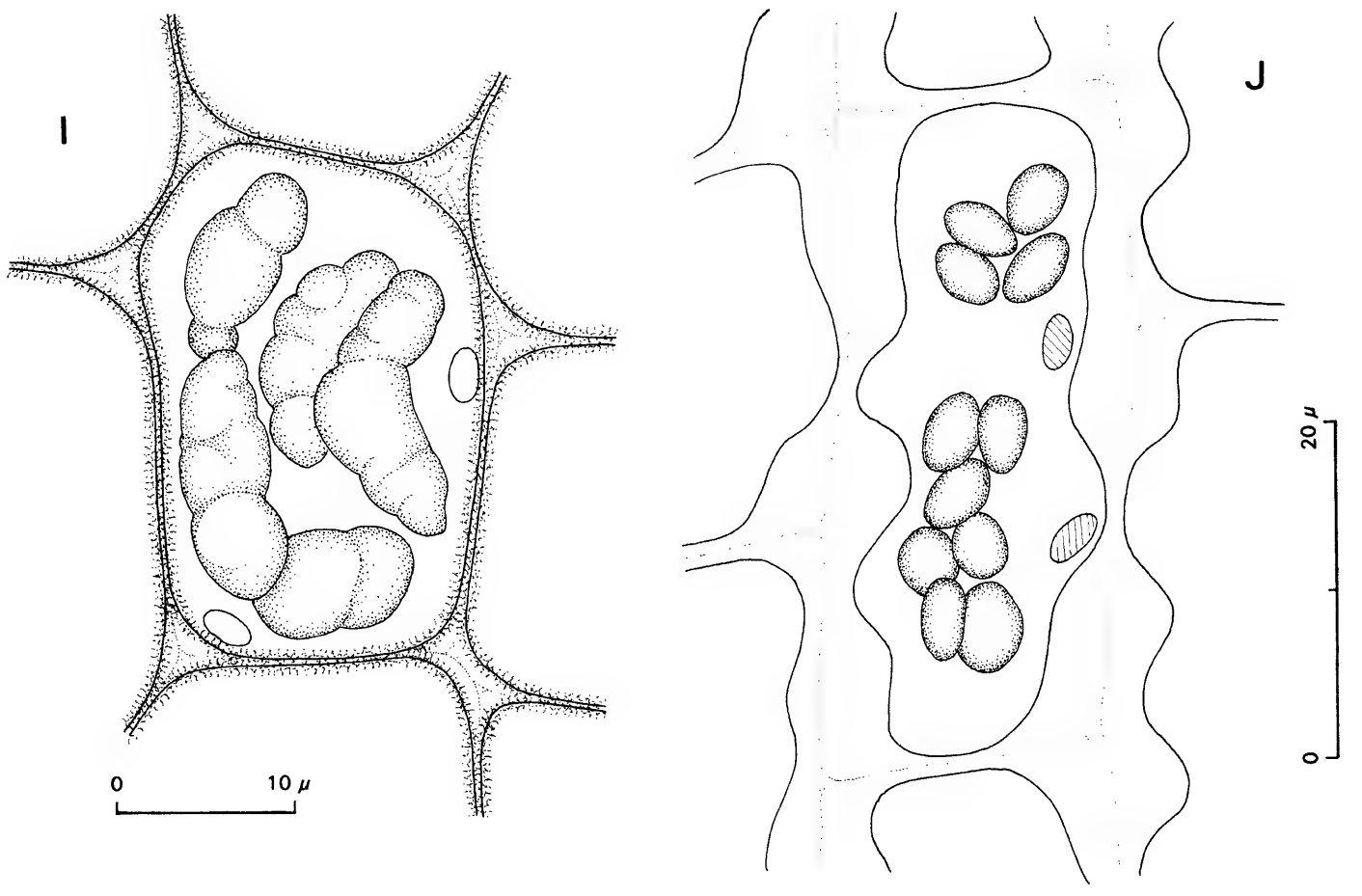
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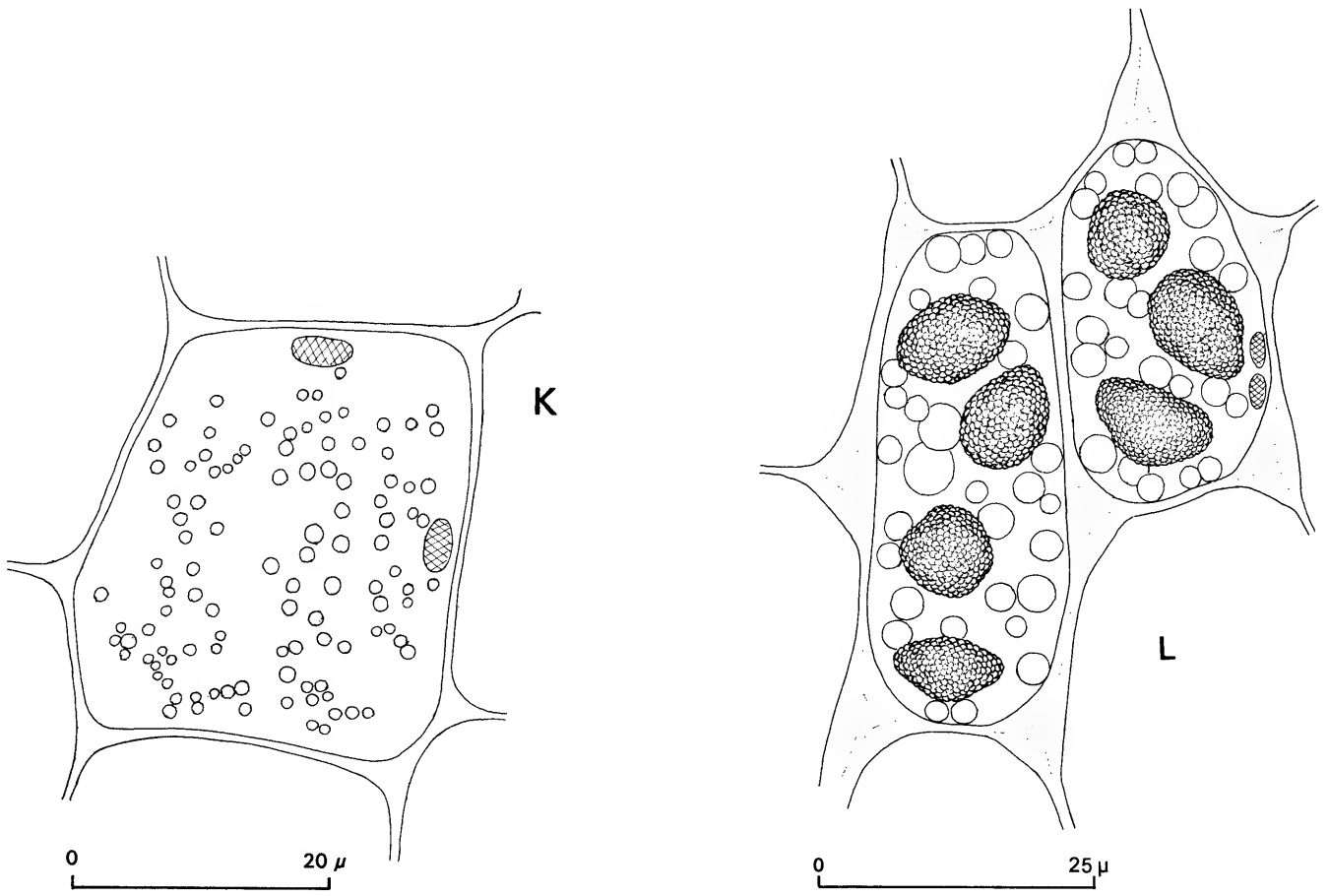
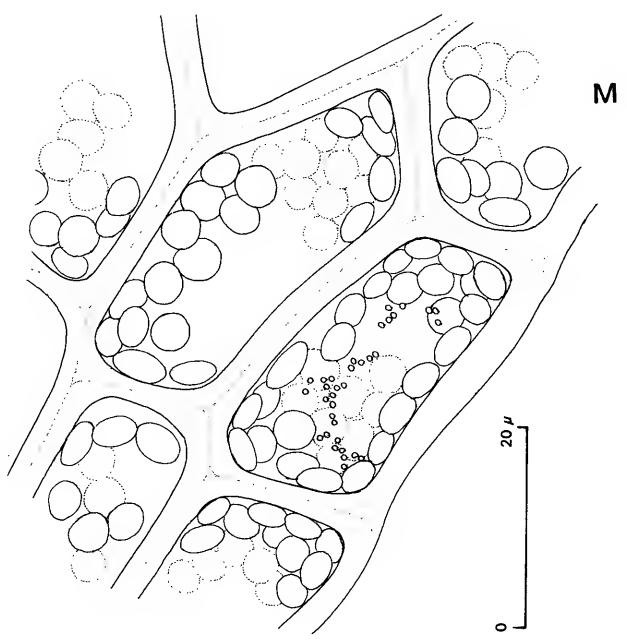


G, *Acromastigum mooreanum*; and H, *Leptoscyphus* sp.); the coarsely botryoidal oil-bodies each appear like a cluster of grapes. Breakup is similar to the papillose condition.

homogeneous: either with no internal segmentation or with isolated incomplete or complete segments (e.g., *Bazzania* spp.), and the outer surface is smooth (Examples I, *Bazzania tayloriana* and J, *Herbertus oldfieldianus*). Oil-bodies may have some internal differences in "cloudiness," probably due to differences in oil viscosity.

minute and numerous: the "Schrot-Korn Typus" of Müller (1939); oil-bodies are homogeneous and commonly only a few microns in diam. (Example K, *Metahygrobiella drucei*).

oil-bodies dimorphic: presence of two different oil-body types within the same cell, e.g., *Trichotemnoma corrugatum* has oil-bodies in all leaf cells, but dimorphic within each cell: one type occurs 2–4 per median leaf cell, burnt orange-brown, large, coarsely granular to finely papillose and irregular in shape; the other type is hyaline, numerous per cell, ± spherical, homogeneous, smooth, much smaller (only 1–1.9 μm), and occurs in the outer



part of the cytoplasm (Example L, *Trichotemnoma corrugatum*). The size of the "grains" or "spherules" is much different, i.e., the "spherules" in the outer part of the cytoplasm do not originate from breakdown of the much larger other type.

cells dimorphic: presence of oil-bodies in some cells, while other cells completely lack them.

oil-bodies absent: We have placed species in this category if oil-bodies are lacking altogether (e.g., *Megalembidium*) or if only scattered minute lipid droplets are present (e.g., Example M, *Drucella*).

In some cases oil-body color is difficult to establish with certainty. Gradations occur from a hyaline, glistening condition to a smoky-grey, dull and opaque condition. Extremes of each condition are very distinct with regard to color and brightness. Intermediates, however, are more difficult to adequately and definitively describe. The color of brownish oil-bodies is often especially distinct at lower magnifications (e.g., at 200× or 400×).

The type of fungal component present in a New Zealand liverwort is included and placed at the end of the gametophyte description. The data have been kindly provided by Jeffrey Duckett, and details of some of the liverwort–fungi associations may be found in the account in Section 12 below and in papers cited there.

Bibliography

The bibliography section in this volume attempts to be comprehensive and includes references that we consider of interest to the student of New Zealand hepatics. It includes references cited in this volume as well as those that are not. The Literature Cited sections for volumes 2 and 3 will include only references cited in those volumes.

12. Endophytic fungi in New Zealand liverworts

Jeffrey G. Duckett and Roberto Ligrone

Introduction

Liverworts contain a wide range of endophytic fungal associations matching mycorrhizas in higher plants. Although the existence of these associations had been known since the nineteenth century, it is only over that past 25 years or so that the groups of fungi have been identified by electron microscope studies (Duckett et al., 1991, 2006a) and most recently the fungal genera by molecular sequencing (Bidartondo et al., 2003; Kottke et al., 2003; Russell and Bulman, 2005; Upson et al., 2007). While axenic culturing of both partners in these associations and reinfection experiments are providing data on the host ranges of the fungi (Duckett and Read, 1995; Duckett et al., 2006a; Pressel et al., 2008) that in some cases extend to adjacent vascular plants, their functional significance has yet to be investigated (Read et al., 2000; Selosse, 2005).

The present account is based on detailed sampling of all the different major groups of liverworts collected during two visits to New Zealand in 1999 and 2001. All the specimens were examined in the living condition by light microscopy immediately after collection, whereas key taxa were subsequently studied by electron microscopy. The overall distribution of fungi in New Zealand liverworts closely mirrors that from earlier surveys of Northern Hemisphere taxa. However, this survey also provides new information on numerous taxa

whose fungal status was previously unknown, as this information is completely lacking in Allison and Child (1975). Although our sampling included over 90 genera, it was far from exhaustive. Nevertheless, the general overview presented here is unlikely to change radically, although observations on additional taxa will doubtless reveal some surprises, particularly among the *Jungermanniales*.

The distribution of fungi across New Zealand liverworts presents a remarkably complete snapshot of the distribution of these associations worldwide; the only notable absences from New Zealand being the *Blasiales* and *Sphaerocarpales* (both fungus-free), the *Pelliineae* (typical glomeromycotes), the *Arnelliaceae* (distinctive basidiomycetes) and the *Pleuroziaceae* (fungus-free).

Marchantiales

All the New Zealand members of the *Marchantiales*, including *Neohodgsonia* and *Monoclea* but with the exception of the *Ricciaceae*, which lack endophytes (as is the case in the rest of the world), contain associations with glomeromycote fungi cytologically very similar to Paris-type vesicular arbuscular mycorrhizas formed by higher plants (Ligrone et al., 2007). The fungi occur in specific ventral cell layers in the midrib region throughout the thalli and in the smooth but not the pegged rhizoids. The endophytes do not, however, extend into the growing apices of the thalli and are also absent from the oil-body–containing cells, from around the sex organs and placental regions, and from the sporophytes. Hyphae have multiple entry sites into the rhizoids, from which they spread into the thallus cells proper. The fungi are entirely intracellular, with large infecting hyphae (Fig. 2a; trunk hyphae) spreading directly through the walls from cell to cell where they form numerous arbuscules comprising much-branched fine hyphae (Fig. 2a) and occasional multinucleate smooth-walled vesicles (Fig. 2b). Ubiquitous in the glomeromycote infections in liverworts (Duckett et al., 2006b) and also in pteridophytes, including both the gametophytes and sporophytes of *Psilotum* and *Tmesipteris* in New Zealand (Duckett and Ligrone, 2005), is the presence of gram-positive-like bacteria within the fungi (Fig. 2d).

Fungus colonization causes major changes in the host cells, including proliferation of the cytoplasm mitochondria and endoplasmic reticulum, replacement of a large central vacuole by numerous small ones, migration of the nucleus from a peripheral to a central location and a dramatic reduction in the starch content of the plastids. In later infection stages the arbuscules degenerate (Fig. 2c), and frequently a second colonization cycle can be seen.

This scenario for the fungi found in New Zealand *Marchantiales* is very much in line with expectation from previous information on Northern Hemisphere taxa (Read et al., 2000). The recent demonstration of a common endophyte (*Glomus* species) in New Zealand *Marchantia foliacea* and *Podocarpaceae* (Russell and Bulman, 2005) now invites experiments on possible nutrient sharing via the fungus as has been demonstrated previously between *Cryptothallus* and *Betula* in the Northern Hemisphere (Bidartondo et al., 2003).

Metzgeriales

The present survey produced some novel and highly distinctive results for the *Metzgeriales*. Strikingly similar to the marchantialean glomeromycote infections are the associations found throughout the families of the *Metzgeriales* now grouped together as *Metzgeriidae* clade I, viz. *Fossombroniaceae*, *Allisoniaceae*, *Pallaviciniaceae* and *Hymenophytaceae* (Crandall-Stotler

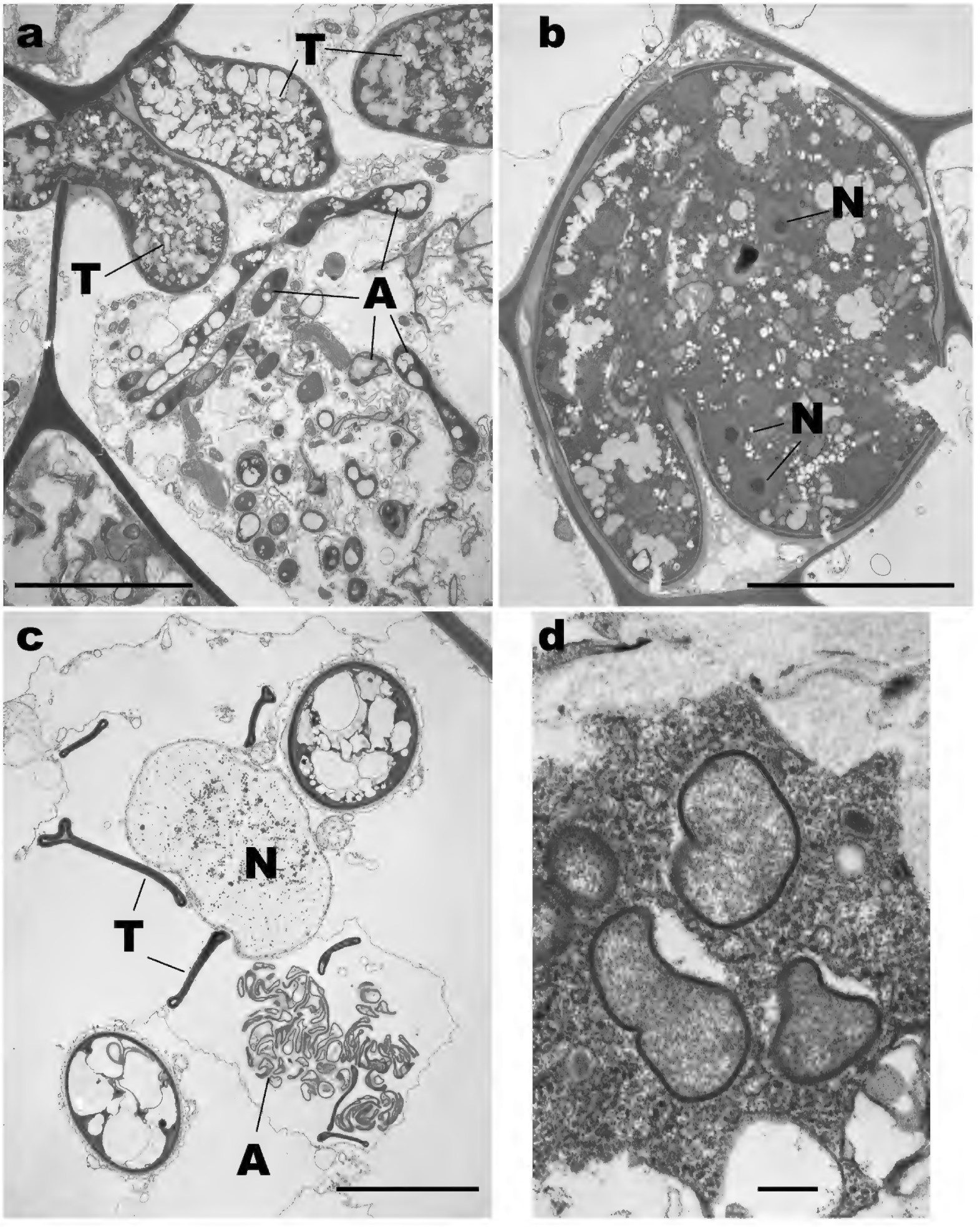


Fig. 2.
Transmission electron micrographs of *Marchantia foliacea* illustrating typical features of glomeromycote associations in New Zealand *Marchantiales* and *Metzgeriales.* a. Early infection stage showing numerous arbuscules (= A) and trunk hyphae (= T). b. Multinucleate fungal vesicle filling a host cell (N = nuclei). c. Late infection stage showing collapsed trunk hyphae (= T) and arbuscules (= A) (N = host cell nucleus). d. Gram-positive bacteria typical of all liverwort glomeromycote fungi. Scale bars: 10 μ (a, b), 5 μ (c), 200 nm (d).

et al., 2005; Forrest and Crandall-Stotler, 2004, 2005; Ligrone et al., 2007). Whereas in the first two families, as in the *Marchantiales*, they occur right up to the thallus apices within specific ventral cell layers, in the last two they are restricted to the subterranean rhizomatous axes lacking lateral laminae (Ligrone et al., 2007). The widespread occurrence of fungi in these axes has not been noted previously, indeed *Hymenophyton* was previously considered fungus-free (Nebel et al., 2004). In *Metzgeriidae* clade II fungi are absent from the basal genus *Pleurozia* (not present in New Zealand) and from *Phyllothallia* and *Metzgeriaceae*, while the *Aneuraceae* contain basidiomycetes (Fig. 3c) whose cytology, like that in Northern Hemisphere *Aneura pinguis* and *Cryptothallus*, is almost identical to orchidaceous mycorrhizas (Ligrone and Duckett, 1993). The fungi form hyphal coils within the host cells (Fig. 3b) that are then digested by the host (Fig. 3a). Multiple infection cycles are frequent. In each taxon the fungi occupy highly specific layers in the ventral region of the thallus. In *Verdoornia* all the cells in the ventral half of the thalli are infected (Fig. 3a, b), as is also found in *Aneura pinguis* in the Northern Hemisphere. In New Zealand *Aneura* species, however, the endophytes are restricted to 2–3 ventral cell layers (Duckett and Ligrone, 2008). In contrast to *Aneura* the vast majority of New Zealand *Riccardia* species are fungus-free, as is the case for all the European members of the genus. Exceptions are *R. pennata*, with prominent hyphae restricted to the ventral epidermal cells, and *R. intercellula*, where uniquely the hyphae lie within the inner walls of the ventral epidermis (Brown and Braggins, 1989). These highly distinctive fungal distributions are invaluable aids in identification.

Jungermanniales

Glomeromycote infections are unknown in leafy liverworts, and in New Zealand most families lack fungi, as is the case in the rest of the world. A few families, however, contain basidiomycetes, with ascomycetes being distributed more widely. The former associations would appear to be more restricted in the New Zealand flora compared with the Northern Hemisphere (Duckett et al., 2006a), and the only genuine examples to date are *Diplophyllum* (Fig. 3d, e) and *Lophozia*. A distinctive feature of these associations is their occurrence as a mosaic of infected and uninfected cells within the central cells of the stems and the absence of hyphal digestion by the hosts. Further studies are now needed to identify putative basidiomycetes in other genera in the *Scapaniaceae* and in *Lethocolea pansa*, where the purple-walled cells occupying the ventral half of the stems are packed with septate hyphae. Why many other leafy liverworts with swollen stems that grow on apparently highly suitable substrata, often in very close proximity to glomeromycote-containing thalloid genera, are fungus-free is a mystery.

Ascomycetes occur in the swollen rhizoids in most New Zealand genera in the *Lepidoziaceae*, *Calypogeiaceae*, *Cephaloziaceae* and *Cephaloziellaceae*. They are particularly prominent on flagelliform axes (also see Duckett et al., 1991) that may extend for tens of centimeters into peaty substrata. Indeed the prominence of these axes is perhaps one of the most distinctive features of New Zealand *Lepidoziaceae*. Whether the branched rhizoids in *Acromastigum* and *Bazzania*, which are also most prominent on flagelliform branches but rarely extend deep into the substratum, also form a functional relationship with fungi or are colonized only after death urgently requires investigation. The same is also true for the rhizoids on the rhizome systems in the *Adelanthaceae*. Swollen, fungus-packed rhizoids of unconfirmed identity are also a characteristic feature of the *Balantiopsaceae*, in contrast to the fungus-free rhizoids in members of the *Jungermanniaceae* that often grow with them.

The most surprising discovery of the present survey was that the highly distinctive branched

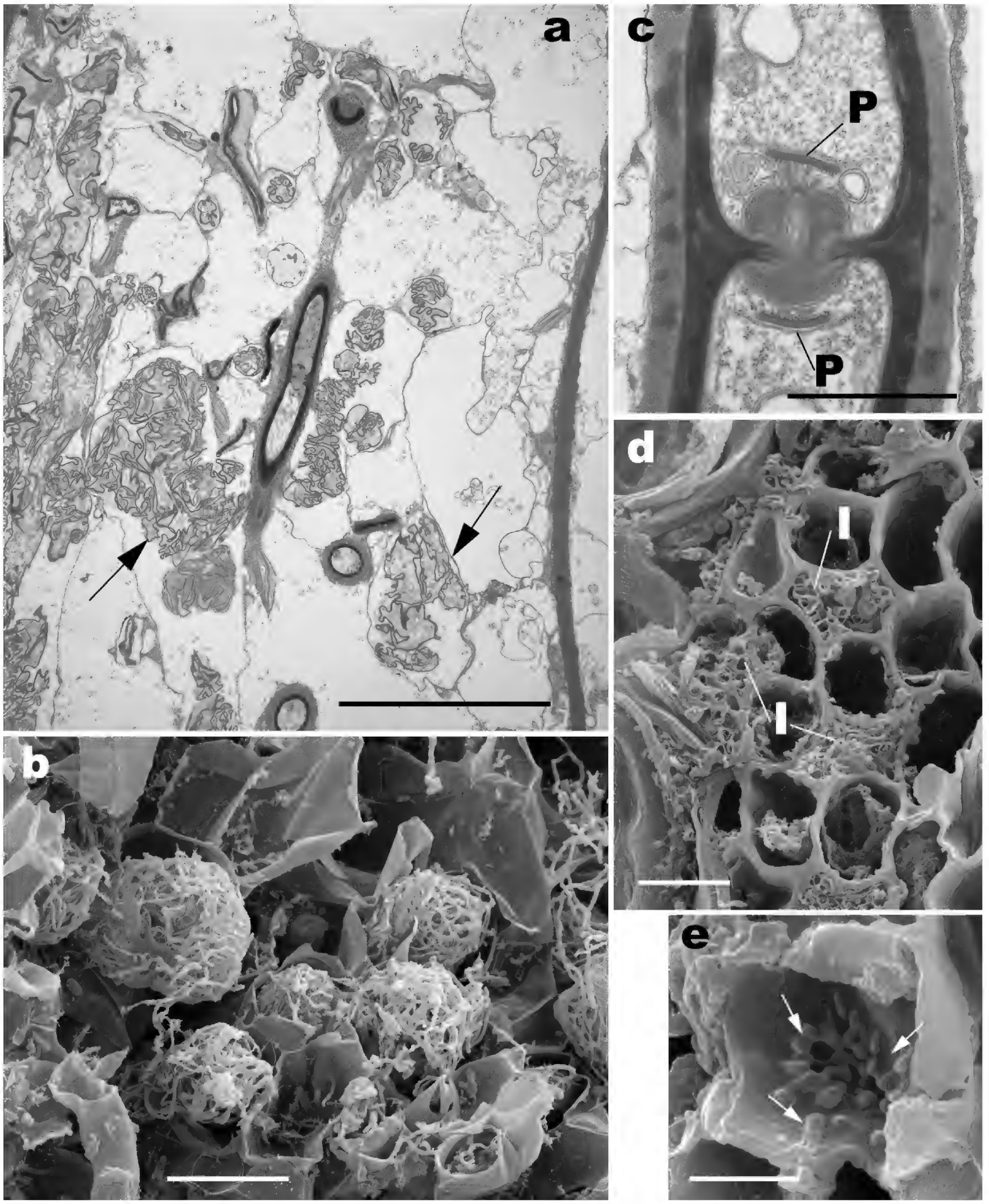


Fig. 3.
Transmission (a, c) and scanning (b, d, e) electron micrographs illustrating typical features of basidiomycete associations in New Zealand liverworts. a–c. *Verdoornia succulenta.* a. Heavily infected cell containing a mixture of healthy and collapsed hyphal masses (arrowed) from an earlier infection cycle. b. Hyphal coils in host cells. c. Dolipore septum with imperforate parenthosomes (= P) typical of all basidiomycetes in liverworts. d, e. *Diplophyllum dioicum.* d. Ventral part of a stem showing a mosaic of infected (= I) and uninfected cells. e. Ingress of hyphae into uninfected cells is prevented by overgrowths of host cell wall (arrowed). Scale bars: 10 μ (a, e), 20 μ (b, d), 1 μ (c).

and septate rhizoids in the *Schistochilaceae* are packed with fungi (Pressel et al., 2008). Electron microscopy identified the fungus as an ascomycete confirmed from sequencing as *Rhizoscyphus ericae*, the mycobiont in the *Ericales*. Culturing experiments have demonstrated that rhizoid branching and septation is in fact induced by this fungus, whereas apical branching without divisions in the rhizoids of other liverworts occurs as a consequence of contact with solid substrata.

Haplomitrium and Treubia

The glomeromycote associations found in *Haplomitrium* and *Treubia* are unique among liverworts and vascular plants (Carafa et al., 2003; Duckett et al., 2006b). Indeed *Treubia* contains one of the most highly differentiated symbiotic fungal associations in land plants. Unlike other liverworts in which thallus differentiation is dependent on cells of different sizes, wall thickness and the conducting strands, the unique anatomy of *Treubia* axes depends almost entirely on different host-fungus zones. Though differing in a few details, a suite of commonalities closely links the fungal associations of the two groups. *Haplomitrium* and *Treubia* are unique among liverworts in secreting huge quantities of mucilage. This is exuded directly from the epidermal cells lining the leafless subterranean axes in *Haplomitrium*, and from clefts between these cells from mucilage-filled intercellular spaces within the thalli in *Treubia.* Unlike the Golgi body–derived secretions from apical mucilage papillae in other liverworts, the mucilage in *Haplomitrium* and *Treubia* is a direct product of the endoplasmic reticulum. Within the mucilage spaces in the center of the *Treubia* thallus, the fungus proliferates to form pseudo-parenchymatous hyphal masses (Fig. 4c) and, in older thalli, highly distinctive spores with thick multilayered walls (Fig. 4d). The latter also occur within the mucilage surrounding the subterranean axes in *Haplomitrium*. Hyphae are obviously not associated with rhizoids in *Haplomitrium*, which lacks this feature, and *Treubia* is the only fungus-containing liverwort in which hyphae are absent from the rhizoids. In both genera the endophytes enter the epidermal cells directly, and in both the fungus has a very similar intracellular phase. In *Haplomitrium* the epidermal and subepidermal cells are packed with arbuscule-forming hyphae and short-lived fungal lumps (Fig. 4a) clearly distinct from the vesicles in other liverworts and vascular plant glomeromycotes. Exactly the same fungal lumps occur in the ventral cell layers in the *Treubia* thallus below the extracellular fungal zone (Fig. 4b). It is interesting to recall that in his original meticulous description of the endophyte in *Treubia*, Goebel (1891) speculated that the inter- and extracellular phases might be different fungi. Electron microscopy over a century later was needed to demonstrate hyphal continuity between the two, thus proving these to be one and the same fungus.

Ecological considerations

Correlations between ecology and the presence or absence of fungi in New Zealand liverworts also mirrors the situation in rest of the world (Duckett et al., 2006a). Leafy taxa with rhizoidal ascomycetes are most often found on waterlogged, humus-rich substrata, particularly peaty soils and rotting wood, whereas thalloid taxa are most frequently found growing on mineral soils. Few or no epiphytes contain endophytes (e.g., they are unknown in the *Lepidolaenaceae*, *Porellaceae*, *Frullaniaceae* and *Lejeuneaceae*), and the same is true of species growing directly on bare rocks, e.g., *Gymnomitriaceae*. Turning to anatomy, fungi are generally lacking in taxa with highly thickened stem cell walls and with erect stems bearing few or no rhizoids, e.g., *Herbertus*, *Triandrophyllum*, *Trichocolea*, *Ptilidiinae* and *Lepidolaenaceae*. Perhaps the

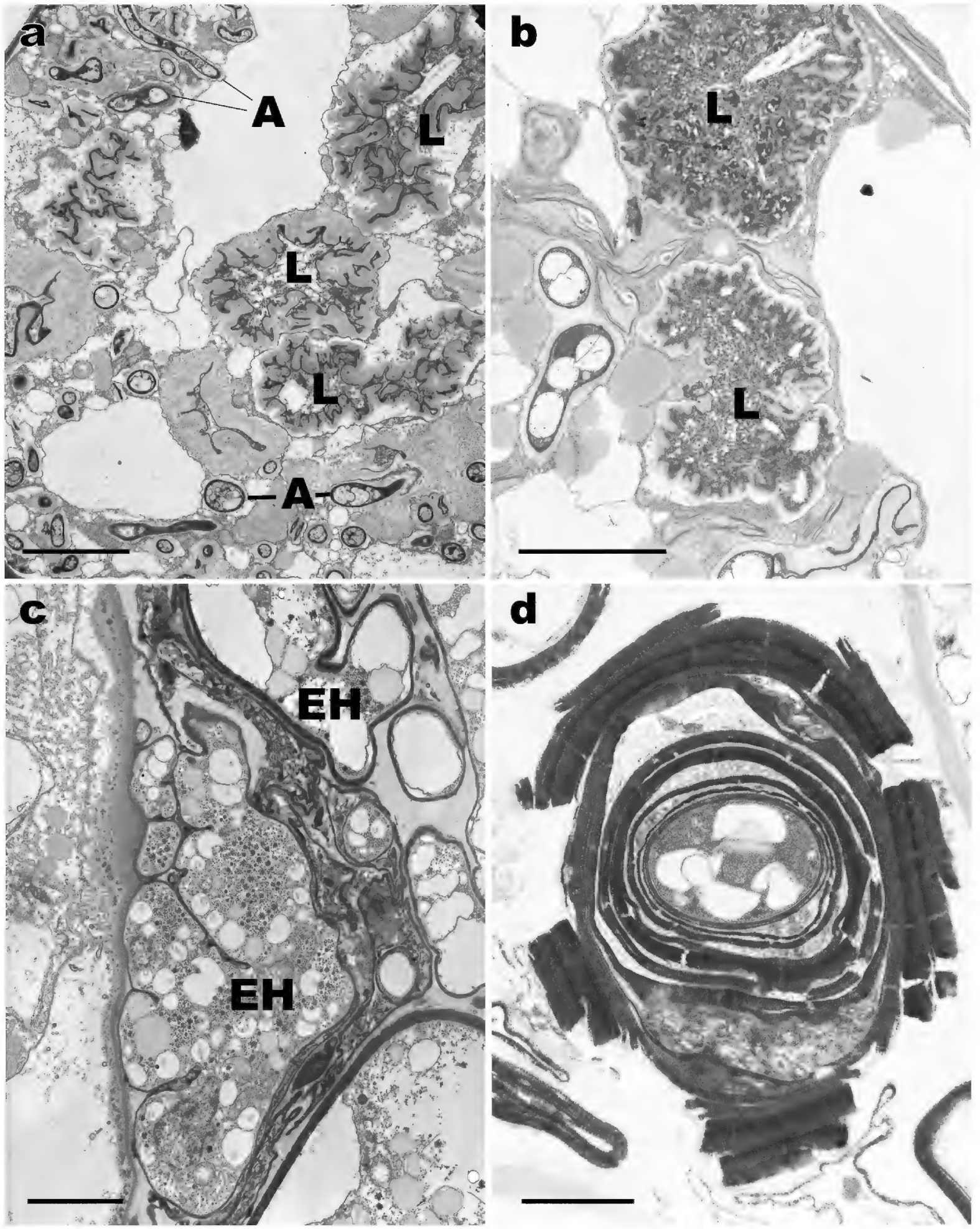


Fig. 4.
Transmission electron micrographs of the unique features of the fungal associations in *Haplomitrium* and *Treubia.* a. *Haplomitrium gibbsiae,* fungal arbuscules (= A) and lumps (= L) in a heavily infected epidermal cell from a subterranean axis. b, c. *Treubia lacunosa.* b. Fungal lumps (= L) in a ventral thallus cell. c. Pseudoparenchymatous extracellular hyphae (= EH) in mucilage-filled intercellular spaces within a thallus. d. *Treubia pygmaea.* Fungal spore with a very thick multilayered wall in a mucilage-filled intercellular space. Scale bars: 5 μ (a, b), 2 μ (c), 1 μ (d).

most surprising fungus-free taxa, given their apparently suitable ecology and anatomy, are *Goebelobryum*, *Jamesoniella*, *Marsupidium* and *Solenostoma.*

Evolutionary considerations

A particularly interesting aspect of the liverwort and hornwort fungus associations is the new insights they are providing in liverwort classification and phylogeny and in the evolutionary origins of plant symbioses. Such considerations have become all the more significant since the almost unanimous recognition that liverworts are the earliest divergent clade of land plants (Renzaglia et al., 2007) and, more surprisingly, new molecular (Groth-Malonek et al., 2004) and immunocytochemical evidence (Carafa et al., 2005) positions the hornworts as sister to vascular plants. When considered against traditional liverwort classifications, the distribution and evolution of the fungal associations seem to make little or no sense with an almost random presence or absence of glomeromycetes, basidiomycetes or ascomycetes.

The twenty-first century has witnessed the first detailed molecular and total evidence liverwort phylogenies, and with these have come major advances in our understanding of the liverwort phylogenetic tree. The topology of the tree shows *Treubia* and *Haplomitrium* closely nested in a clade sister to all other land plants. It is perhaps not surprising therefore that their fungal associations share so many common features. The absence of fungi in *Blasiales* and *Sphaerocarpales*, the two clades immediately above *Treubia* and *Haplomitrium* and sister to all other liverworts, suggests the loss of the primeval associations and the secondary acquisition of the typical glomeromycote associations found throughout the *Marchantiopsida* and clade I in the *Metzgeriidae*. The topology of recent liverwort phylogenies (Forrest and Crandall-Stotler, 2005) strongly suggests that these typical associations with glomeromycotes long predated arbuscular mycorrhizas and that those in *Haplomitrium* and *Treubia* are the most ancient of all extant land plant–fungal symbioses.

The ascomycetes in leafy liverworts may then be considered to be a secondary acquisition of more recent origin following the loss of the primitive glomeromycote associates. Recent dating of the *Schistochilaceae*, the sister family to all other fungus-containing leafy liverworts (Heinrichs et al., 2007), in the Triassic 250 Mya suggests these long predated ericalean mycorrhizas, their vascular plant counterpart, dated at 106–114 Mya (Wikström et al., 2001), and whose endophytes they share (Read et al., 2000).

In leafy liverworts basidiomycete associations are most likely another example of secondary acquisition following the loss of ascomycetes. But, here again, the identification of their fungi as members of the *Sebacinaceae* (Kottke et al., 2003) suggests ancient origins. In contrast, the identification of the basidiomycetes with very different cytology in the *Aneuraceae* as *Tulasnella* (Bidartondo et al., 2003; Kottke et al., 2003; Nebel et al., 2004) indicates these to be much more recent. This finding is very much in line with this family forming the crown group in *Metzgeriidae* II (Crandall-Stotler et al., 2005). The final revelation from marrying fungi and phylogeny is the presence of a typical aneuracean basidiomycete in *Verdoornia*. This monotypic New Zealand genus, originally regarded as isolated and primitive (Schuster, 1964d, 1999d), is now nested within the *Aneuraceae* (Crandall-Stotler et al., 2005).

Mosses and hornworts

In concluding this account it must be emphasized that one of the most striking yet not widely cited differences between liverworts and mosses is that, in the latter, mutualistic fungal associations of any kind are unknown (Renzaglia et al., 2007). In hornworts, however, glom-

eromycote associations that are cytologically closely similar to those in thalloid liverworts have been noted in a few species, although their overall distribution requires further study (Read et al., 2000). The picture from New Zealand may well turn out to reflect the situation worldwide. We found the invariable presence of glomeromycote infections to be identical to those described from the Northern Hemisphere *Phaeoceros carolinianus* (Ligrone, 1988): in *Anthoceros laminiferus*, *Phaeoceros coriaceus* and *P. hirticalyx*. These are absent in *Dendroceros validus* and *D. granulatus*, mirroring the absence of fungi in epiphytic liverworts. Endophytes are also absent from the three New Zealand *Megaceros* species examined here (*M. denticulatus*, *M. pellucidus* and *M. giganteus*), again paralleling fungus-free liverworts growing in very wet habitats. It is noteworthy that the basal genus *Leiosporoceros* apparently lacks an endophyte (Villarreal and Renzaglia, 2006). Although at present highly provisional, when superimposed on the most recent hornwort phylogeny (Renzaglia et al., 2007), the endophyte distribution strongly suggests secondary acquisition of glomeromycetes independently of those in thalloid liverworts.

Genera examined

The order of genera follows Glenny (1998). A, ascomycete; B, basidiomycete; G, glomeromycote; ?, fungus of unknown identity; NP, fungus not present.

Anthoceros G, *Dendroceros* NP, *Megaceros* NP, *Phaeoceros* G, *Haplomitrium* G, *Lepicolea* NP, *Herbertus* NP, *Triandrophyllum* NP, *Trichotemnoma* NP, *Archeophylla* NP, *Temnoma* NP, *Trichocolea* NP, *Acromastigum* ?, *Bazzania* ?, *Chloranthelia* A, *Hygrolembidium* A, *Isolembidium* A, *Kurzia* A, *Lembidium* A, *Lepidozia* A, *Megalembidium* A, *Neogrollea* A, *Pseudocephalozia* A, *Psiloclada* A, *Telaranea* A, *Zoopsidella* A, *Zoopsis* A, *Calypogeia* A, *Adelanthus* ?, *Wettsteinia* ?, *Cephalozia* A, *Cephaloziella* A, *Anthelia* NP, *Anastrophyllum* NP, *Chandonanthus* NP, *Cryptochila* NP, *Jamesoniella* NP, *Jungermannia* NP, *Lophozia* B, *Gymnomitrion* NP, *Herzogobryum* NP, *Marsupella* NP, *Diplophyllum* B, *Chiloscyphus* NP, *Clasmatocolea* NP, *Heteroscyphus* NP, *Leptoscyphus* NP, *Saccogynidium* NP, *Plagiochila* NP, *Plagiochilion* NP, *Acrobolbus* NP, *Goebelobryum* NP, *Lethocolea* ?, *Marsupidium* NP, *Tylimanthus* NP, *Pachyschistochila* A, *Paraschistochila* A, *Schistochila* A, *Balantiopsis* ?, *Eoisotachis* ?, *Isotachis* ?, *Radula* NP, *Ptilidium* NP, *Dendromastigophora* NP, *Gackstroemia* NP, *Lepidogyna* NP, *Lepidolaena* NP, *Porella* NP, *Frullania* NP, all genera of *Lejeuneaceae* NP, G, *Austrofossombronia* G, *Fossombronia* G, *Phyllothallia* NP, *Allisonia* G, *Verdoornia* B, *Pallavicinia* G, *Podomitrium* G, *Symphyogyna* G, *Xenothallus* G, *Hymenophyton* G, *Aneura* B, *Riccardia* B and NP, *Metzgeria* NP, *Monoclea* G, *Targionia* G, *Lunularia* G, *Dumortiera* G, *Asterella* G, *Reboulia* G, *Marchantia* G, *Neohodgsonia* G, *Riccia* NP.

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Order 1. **CALOBRYALES** Campb.

Plants leafy, erect, fleshy and soft-textured, occasionally brittle, growing either as individuals or loosely gregarious, rarely forming extended patches, bright grass-green to yellowish green, lacking secondary pigments (except for antheridial walls), mostly 8–25 mm tall, growing by an apical cell with 3 nearly equal cutting faces, fundamentally triradial, varying from radially symmetric to anisophyllous (then with the third, reduced row of leaves dorsal). Branching copious, very irregular, exogenous-intercalary (the branch potentially originating from any ± mature, cortical cell), from all 3 rows of merophytes, resulting in a system of 3 types of shoots: ± horizontal, leafless, pale, rhizomatous axes, from which leafy branches may arise (or which may be gradually converted into erect, leafy axes); erect, leafy stems; geotropic, leafless stolons or flagella. Mucilage (slime) papillae conspicuous, of the stalked type, secreting massive amounts of mucilaginous matter. Axis terete, massive, often brittle and very fleshy, without a defined cortex, with a ± distinct central strand of smaller, elongated, leptodermous cells and a peripheral, parenchymatous, chlorophyllose cortical region. Rhizoids lacking. Leaves not passing through an embryonic 2-lobed stage, 3-ranked, gradually larger above or (sometimes) abruptly larger, the basal parts of leafy shoots microphyllous or leafless, the insertion transverse or ± succubous (then the third, often smaller, dorsal row of leaves remaining transversely inserted, the insertion line often acroscopically arched and laterally decurrent); leaves soft-textured and often brittle, unistratose or 2–3(4)-stratose only toward base, variable in shape, elliptical to broadly orbicular-subreniform to obovate-obdeltoid, in *Haplomitrium ovalifolium* sometimes bifid to the base into linear-lingulate lobes, the leaves entire or subentire. Cells non-collenchymatous, soft, relatively large, thin-walled. Oil-bodies distinct, small for cell size, several to many (to over 100) per cell, essentially homogeneous (when minute) to granular, colorless to pale brownish. Asexual reproduction absent.

Dioecious (autoecious in *Haplomitrium monoicum*). Antheridia numerous, fundamentally axillary, in axils of uppermost ♂ bracts, the ♂ bracts sometimes reduced to 3, then antheridia seemingly aggregated in a central group (disc) at summit of axis, which may be somewhat dilated, or, at times, a few scattered and arising some distance from leaf axils; antheridia (mature) yellowish or orange-red, mature antheridia clavate, the body gradually narrowed into stalk, the stalk elongate, 4-seriate. Archegonia with basically an identical disposition (and similar early ontogeny, see Schuster [1966b, 1967d]), aggregated (at least initially) in a terminal group on a dilated disc, situated fundamentally in the axils of the 3 uppermost leaves (but sometimes with scattered, reduced, lingulate "bractlets" between the archegonia), with archegonium production always resulting in swelling of the shoot tip, the archegonial development not involving apical cells (thus technically anacrogynous, and with absence of fertilization the shoot usually continuing growth); archegonia with neck extremely elongate, formed of 4 cell rows, the neck long, with 16–20(40) neck-canal cells, venter only slightly greater in diameter than neck at maturity. Archegonial venter dividing extensively periclinally subsequent to fertilization, forming a fleshy, cylindrical, green to yellowish, brittle, massive calyptra, the calyptra smooth and with unfertilized archegonia basal or nearly so (i.e., a true calyptra), or the unfertilized archegonia elevated on a shoot-calyptra, in either case the calyptra not surrounded by any protective device (involucres, perianth, marsupium, etc.). Fertilization of 1 or 2–3 archegonia per inflorescence may occur and 1 or 2–3 sporophytes per plant may result (the initial embryo formed not suppressing development of additional sporophytes).

Seta elongating capsule far beyond shoot-calyptra, notably massive, with a ± vestigial central strand of smaller cells. Capsule ellipsoidal-cylindrical, the wall 1-stratose (only the apical portion bistratose), the wall each with 1(2) annular, narrow, longitudinally oriented thickening bands; dehiscence usually imperfect and lateral (i.e., with lateral slits), often with 2 or 1 dehiscence lines, the capsule apex remaining fused and indehiscent.

Spores normally 16 per elater, 17–30 μm in diam., granulate to weakly reticulate; spore-elater ratio ca. 3:1. Elaters long, very slender and markedly attenuate, 6–10 μm in diam., gradually and only feebly tapered, usually with 2 narrow, yellowish spirals throughout much or all their length. Sporeling development of the *Nardia* type.

The *Calobryales* include relatively few species, all belonging to one family and genus.

Family **HAPLOMITRIACEAE** Dedecek

Haplomitriaceae Dedecek, Arch. Prir. Proskoum. Cech [Prag] 5(4): 17, 71. 1883 ("Haplomitrieae").

The ordinal diagnosis effectively diagnoses the family and the single genus:

Haplomitrium Nees

Scalius Gray, Nat. Arr. Brit. Pl. 1: 704. 1821, *nom. rej.*
Mniopsis Dumort., Commentat. Bot. 114. 1822, *hom. illeg. non Mniopsis* Martius, 1822.
Haplomitrium Nees, Naturgesch. Eur. Leberm. 1: 98, 100, 109. 1833, *nom. cons.*
Calobryum Nees *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 507. 1846.
Rhopalanthus Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 13: 390. 1874.
Scalia Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 532. 1885, *hom. illeg. non Scalia* Sims, 1806.
Steereomitrium E.O.Campb., Mem. New York Bot. Gard. 45: 569. 1987.

Type: *Haplomitrium hookeri* (Sm.) Nees (≡ *Jungermannia hookeri* Sm.)

A genus consisting of some 15 species. The genus is rather widespread in distribution, but the species are, for the most part, restricted in range, as follows: *Haplomitrium ovalifolium* and *H. minutum* (restricted to our area), *H. gibbsiae* (New Zealand, Tasmania), *H. intermedium* Berrie (Australia: New South Wales), *H. chilensis* R.M.Schust. (southern South America), *H. monoicum* J.J.Engel (New Caledonia), *H. blumii* (Nees) R.M.Schust. (Java, Sumatra, New Guinea, Taiwan, Eastern Himalayas of India), *H. giganteum* (Steph.) Grolle (Philippines); *H. mnioides* (Lindb.) R.M.Schust. (Japan, Taiwan), *H. dentatum* (D.Kumar & Udar) J.J.Engel, *H. grollei* D.Kumar & Udar, *H. kashyapii* Udar & D.Kumar and *H. indicum* (Udar & Chandra) R.M.Schust. all from the Darjeeling region of India, *H. hookeri* (Sm.) Nees (Europe, Spitsbergen, West Greenland, eastern North America, western North America, Japan, Eastern Himalayas of India, West Himalayas of India) and *H. andinum* (Spruce) R.M.Schust. (Neotropics).

Affinities of order *Calobryales* are controversial, e.g., Bartholomew-Began (1991) would argue for a common ancestry with *Metzgeriales*. The group has been included in a number of recent phylogenetic studies, with variable phylogenetic position (e.g., Crandall-Stotler and

Stotler, 2000; Forrest and Crandall-Stotler, 2005). We follow Schuster (1966b, 1967d, 2002a) in maintaining a traditional position of the order.

The treatment of this order is adapted and modified from Schuster (1967d, 1971b).

References: Bartholomew-Began (1991; morphogenetics of genus); Campbell (1959, *H. gibbsiae*); Engel (1982a, *H. monoicum* of New Caledonia + general comments); Engel and Schuster (1994, *H. minutum*); Schuster (1967d, rev.; 1971b, *H. ovalifolium*; 2002a).

Key to Species

1a. Plants with stems leafless or microphyllous below, bearing only a few cycles of mature leaves, the leaves rather abruptly larger distally; antheridia in ± definite terminal receptacles, the antheridia never scattered; leaves nearly always broader than long; calyptra massive, a shoot-calyptra, with unfertilized archegonia and bractlets scattered on its surface; vigorous plants, to 16–20(30) mm tall and 6–7.5 mm wide (♀ plants) . . . . . *H. gibbsiae* (p. 63)

1b. Plants leafy throughout their length, bearing a number of cycles of mature leaves, the leaves subequal in size throughout shoot; antheridia in part scattered and indefinite in position, not in terminal receptacles; leaves longer than wide; calyptra smooth, thin, lacking bractlets on surface, the unfertilized archegonia at or near its base; slender and tiny plants 2

2a. Leaves sometimes bifid nearly to base; ♂ bracts and bracteoles arranged in partial spirals, a triquetrous arrangement in androecium lacking; oil-bodies 25–35 per cell, botryoidal. Campbell Is. (60–80 m), South Is. (900–1280 m) . . . . . *H. ovalifolium* (p. 61)

2b. Leaves undivided, never bifid; ♂ bracts and bracteoles in triquetrous arrangement; oil-bodies mostly 11–21 per cell, finely granular. Artificial sites (Turf Research Inst., bowling greens) . . . . . *H. minutum* (p. 65)

Haplomitrium ovalifolium R.M.Schust.

Haplomitrium ovalifolium R.M.Schust., Bryologist 74: 136. *f. 11–29.* 1971. Holotype: Campbell Is., sea cliffs of Mt. Yves Villarceau, ca. 200–275 ft., at Penguin Bay, *Schuster 70-3248* (F!).

Plants isolated to loosely gregarious in growth, slender, clear green, small, the shoots occasionally to 1.5–2.2 mm wide (including the leaves), to 8–16 mm tall. Branching irregular, rather copious; leafy erect axes often with supra-axillary long axes, initially leafless and horizontal, soon erect and leafy (thus 2–3 or more leafy axes clustered together, united by leafless stoloniform sectors); older shoot sectors producing free, often highly elongated, leafless, stoloniform, creeping to geotropic axes. Shoots typically leafy throughout, with lower leaves soon attaining a mature size and form, the leafy shoot thus subequally leafy throughout, except that at and near gynoecia the leaves become moderately larger. Leaves rather rigid, transverse, often obliquely to widely spreading, unistratose except at extreme base, nearly flat, relatively uniform, typically ovate to ovate-lanceolate, the length always clearly greater than width (mostly 1.2–1.5× longer than wide), occasionally bifid nearly to base; apices narrowly rounded to blunt, to bluntly pointed; leaf base only moderately narrowed; margins entire or obscurely

repand to repand-dentate with blunt angulations. Cells opaque, chlorophyllose, thin-walled, the cells in leaf middle from 24–32 × 25–38 μm to (20)25–32(36) × 36–55(60) μm. Oil-bodies (Schuster, 1971b) ca. 25–35 per cell, variable, ± clearly botryoidal, small, from few-segmented to coarsely botryoidal, subspherical and 2.5–2.8(3.5) μm in diam. to ovoid and 2.2 × 3.5 μm to 3–3.2 × 4–5(6.5) μm; chloroplasts averaging subequal to or smaller than oil-bodies in size, ca. 2.5–3.5 × 5–6 μm. Fungal partner a glomeromycote.

Plants dioecious. ♂ Bracts and subfloral leaves often closely juxtaposed lending the ♂ shoots a capitate appearance, a triquetrous arrangement of leaves (and bracts) in androecial region lacking—the arrangement at least imperfectly spiral; the bracts highly variable, but always lingulate to ovate, always narrow, always at least 1.2–1.5× longer than wide, often much longer. Antheridia never in a terminal disc, axillary in bracts, orange-yellow. Gynoecial bracts leaf-like, retaining the narrow form of leaves but slightly larger than leaves, ovate to elliptical to, occasionally, obovate, always clearly longer than wide. Archegonia rather few, typically on the apex of a ± conoidally convex shoot apex subtended by 3 bracts, isolated archegonia occasionally present in the axils of subfloral bracts. Shoot-calyptra cylindrical, small, yellowish green (postmature), seemingly smooth (a single, old shoot-calyptra seen). Otherwise unknown.

Distribution and Ecology: Endemic to New Zealand: Campbell Island, South Island (920–1650 m), North Island (1280 m). Known from Otago (Old Man Ra.), Westland (Mt. Brown, McCullough Pass), Canterbury (The Spike) and Western Nelson (Marino Mtns.).

In the South Island known only from the alpine zone. Unlike *Haplomitrium gibbsiae*, apparently confined to areas that have undergone no human disturbance and, apparently, lacking from forested regions. Found in Nelson on sinkhole walls with *Chionochloa pallens*, *C. australis* and *Marsippospermum gracile*; elsewhere in the South Island under *pallens* and *C. flavescens* tussocks on damp, south-facing aspects. It shares with *H. gibbsiae* a preference for mineral soil rather than humus. It has been found associated with *Brachythecium paradoxum*, *Chiloscyphus subporosus*, *Diplophyllum dioicum*, *Gackstroemia alpina*, *Isotachis intortifolia*, *Marchantia foliacea*, *Megaceros leptohymenius*, *Notoligotrichum australe*, *Pachyschistochila succulenta*, *Riccardia aequitexta*, *Solenostoma totipapillosum*, *Telaranea lindenbergii*, *T. tetrapila* and *Verdoornia succulenta*.

Comments: *Haplomitrium ovalifolium* is a much smaller plant than *H. gibbsiae*, with leaves much longer than wide, basically elliptical in form and widest medially vs. nearly always broader than long and widest in basal 0.25 in *H. gibbsiae*. The leaf form (of regions and/or plants lacking bifid leaves) is much as in *H. minutum*. *Haplomitrium ovalifolium* is unique in the genus in its highly variable form and orientation of the leaves: Androecial shoots show sporadic to frequent leaves that are divided to the base, so that the leaf consists of two autonomous, lingulate segments.

Gametangial position is noteworthy. Antheridia are axillary in leaves and/or bracts when not scattered and are never in terminal groups. Gynoecial shoots have only 6–8 archegonia at the apex of a convex, conoidal shoot tip, but isolated archegonia sporadically are present axillary in subfloral leaves.

Haplomitrium gibbsiae (Steph.) R.M.Schust.

[Plate 1A–C; Fig. 8: 1, oil-bodies, p. 100]

Calobryum gibbsiae Steph., Sp. Hepat. 6: 76. 1917. *Haplomitrium gibbsiae* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 225. 1963. Type: New Zealand, North Is., Wairongamai Mine ("Main"), Te Aroha, 2000 ft., Nov. 1907, *Gibbs 1064 – c. cal.* (G!).

Plants variable, especially in vigor, the leafy shoots isophyllous, arising from a prostrate, irregularly branched, in large part creeping or horizontal, colorless to ivory-colored rhizome that may be coralloid; rhizomatous system with numerous 1–2-celled slime papillae that produce a thick mucilaginous sheath. Leafy stems unbranched above, nearly colorless and leafless below, to 6–7.5 mm wide above (♀ plants), variable in height, to 16–25(30) mm, the shoots above the base with scattered, remote leaves that are rather abruptly larger distally. Leaves bright yellow-green, translucent to opaque, rigid and brittle, 3-ranked and subequal to equal in all ranks, the lateral weakly succubously to almost transversely inserted, variable, often strongly undulate or crispate, widely spreading, unistratose except for a 2–4-stratose basal field, suborbicular-ovate below to deltoid or rhomboidal to rhomboidal-reniform above, commonly bluntly pointed or acute at tips, widest in basal 0.25, nearly always broader than long; margins entire, or, approaching reproductive zones, occasionally with a few low, obtuse, scattered vestigial teeth or ± sinuate-lobulate, the margins with a few scattered slime papillae that are ephemeral and disappear with age. Cells in median sector variable in size from 40–50 μm wide × 45–60 μm long up to 55–65 μm wide × 65–85 μm long. Oil-bodies occupying a small portion of the cell, hyaline, ca. 15–30 to ca. 30–40 per median leaf cell, obscurely finely papillose, sporadically to commonly with a distinct depression, some broad-elliptic to more often long-fusiform to long-crescentic, the tips often becoming protracted (?early stage of breakdown), at times irregular and with 3 protracted tips and triangular in profile, 2–3.5 × 6–11.5 μm. Chloroplasts large for cell size.

Plants dioecious. ♂ Plants with antheridia in ± definite terminal receptacles (but technically axillary in the single cycle of ♂ bracts); androecial plants at times innovating freely from apex of androecium (thus with indeterminate growth), in others not or rarely so. Antheridia numerous (25–45 or more per androecium), at first ivory-white, with age cinnamon, usually with interspersed small bractlets, the stalk 4–10 tiers high. Gynoecium with ca. 20 archegonia aggregated in a terminal receptacle to 7–8 mm across, the gynoecium potentially with indeterminate growth if fertilization does not occur; if fertilization occurs, a shoot-calyptra forms. Gynoecial bracts very variable, rhombic to subrotund or irregularly rhomboid-ovate in outline, often sinuous-crispate, erect, convolute and sheathing the stem-calyptra when young, but usually becoming strongly spreading at maturity. Shoot-calyptra variable, fleshy, rigid, thick-walled, massive, green but becoming whitish green, to 8 mm high or more, the surface with polymorphous lamellae or unistratose teeth, laciniae, or ridges, the ornamentation with age may be in large part deciduous (the surface then smooth), the surface also often with sterile archegonia and slime papillae. Fungal partner a glomeromycote.

Sporophyte usually single, rarely 2 or even 3–4 shoot-calyptrae and sporophytes may form at the apex of a single gametophore. Seta to 20–25 mm long (above perigynium). Capsule ca. 0.5 × 3–4 mm.

Spores ca. 23–29 μm in diam., pale brown, covered with a limited number of compound markings that are irregular, roughened or tuberculate, obovoid to subclavate, strongly elevated, coarse, nipple- to mesa-like, distally often subtruncate and basally often somewhat constricted

(best seen in spore profile); intervening spore coat smooth to locally with small finely tuberculate interstices. Spores tending to cohere in tetrads or diads until maturity, the inner faces much less strongly sculptured. Elaters 7–10 μm wide medially × 280–520 μm long, medially usually 2- sometimes 1-spiral, at times most elaters 1-spiral, the tapered and tortuous ends always 1-spiral.

Distribution and Ecology: New Zealand: Stewart Island (5–30 m), South Island (85–1400 m), North Island (300–1280 m); Australia: Tasmania (rare, cf. Engel [1982a]). Known from Rakiura (Halfmoon Bay area), Fiordland, Otago (Dunedin), Westland, Canterbury (Craigieburn Ra., Arthur's Pass, Upper Rakaia River), Western Nelson, Southern North Island (Tararua Ra.), Volcanic Plateau and Auckland EPs.

Widely distributed in New Zealand; often rather common although rarely in any quantity. Almost always found on fresh mineral soil on soil banks created by roads, tracks, slips, or washouts, either in open sites or under forest (usually *Nothofagus menziesii* or *N. solandri* forest, but also under *Agathis australis* forest at Coromandel). At higher altitudes under dwarf scrub or in herbfield. For instance at Mt. Ruapehu at its North Island upper-altitude limit it was found on a stream bank of volcanic gravel and ash in low scrub of *Dracophyllum recurvum*, *Lepidothamnus laxifolius* and *Gaultheria depressa* var. *novae-zelandiae* with *Triandrophyllum subtrifidum*, and it occurs in high-altitude herbfields in the South Island with *Celmisia angustifolia*, *C. petiolata*, *C. spectabilis*, *Leucogenes grandiceps* and *Ranunculus insignis*.

In just one case recorded from a rotten log in Fiordland with the note "unusual assoc." (CHR 135736). At low altitudes almost always accompanied by *Triandrophyllum subtrifidum* and *Kurzia hippuroides*. Other associated species are *Balantiopsis diplophylla*, *Breutelia elongata*, *Campylopus clavatus*, *Diplophyllum domesticum*, *Distichophyllum pulchellum*, *Ditrichum difficile*, *D. punctulatum*, *Hygrolembidium acrocladum*, *Isotachis intortifolia*, *I. montana*, *Pallavicinia innovans*, *Philonotis scabrifolia*, *Pohlia wahlenbergii*, *Polytrichadelphus magellanicus*, *Solenostoma cryptogynum*, and at higher altitudes in the South Island, *Austrolophozia paradoxa*, *Conostomum pentastichum*, *Jensenia connivens* and *Pachyschistochila colensoana*. The species appears to be a colonizer of new soil surfaces in damp places, and where such sites stabilize, it may be eventually outcompeted by taller vegetation, as indicated by its occurrence on grassy banks in Dunedin, or overtopped by dense *Dendroligotrichum dendroides* on a soil mound in the Craigieburn Ra. This accounts also for its sporadic occurrence and its disappearance from known localities.

Schuster (1967d, p. 45) remarked that the species is clearly "tolerant and ecologically quite unspecialized"—so long "as there is no real danger of periodic desiccation"; it occurs in a "fantastically wide diversity of habitats." We believe, rather, that the species is quite specialized as an early colonizer except in the alpine zone where competition is much less. There is strong consistency in the accompanying species suggesting a fairly precise niche.

Comments: The species is closely allied with *Haplomitrium chilensis* (Schuster, 1971b, figs. 1–10), sharing with that species the rhomboidal to suborbicular leaves and the cohering spores. In *H. chilensis*, however, unfertilized archegonia are situated all or mostly at the base of the calyptra, which is smooth and devoid of bractlets. Spores in *H. chilensis* are larger (32–35 μm in diam. vs. 23–29 μm in *H. gibbsiae*) and bear low tubercules, under 1.5 μm high vs. 2–3 μm high in *H. gibbsiae*. Also, oil-bodies in *H. chilensis* are 20–28 per cell, ca. 4–5 × 4–6 μm vs. 32–50 or more per cell and notably smaller in *H. gibbsiae*. Some authors treat these species as conspecific (e.g., Hässel and Solari, 1976; Bartholomew-Began, 1991).

Bartholomew-Began (1991) placed four Indian taxa into synonymy of *Haplomitrium gibb-*

siae; we agree with the comment in Schuster (2000a, p. 30) that "this remains to be convincingly demonstrated."

Haplomitrium minutum (E.O.Campb.) J.J.Engel & R.M.Schust.

[Fig. 5]

Steereomitrium minutum E.O.Campb., Mem. New York Bot. Gard. 45: 569. 1987. *Haplomitrium hookeri* var. *minutum* (E.O.Campb.) Barthol.-Began, Bryophyt. Biblioth. 41: 230. 1991. *Haplomitrium minutum* (E.O.Campb.) J.J.Engel & R.M.Schust., Bryologist 97: 65. 1994. Holotype: New Zealand, North Is., Performance trial plots, Turf Research Institute, nr. Palmerston North (*non vidi*); isotypes: (MPN ["duplicate of MPN 16015"]!, NY!).

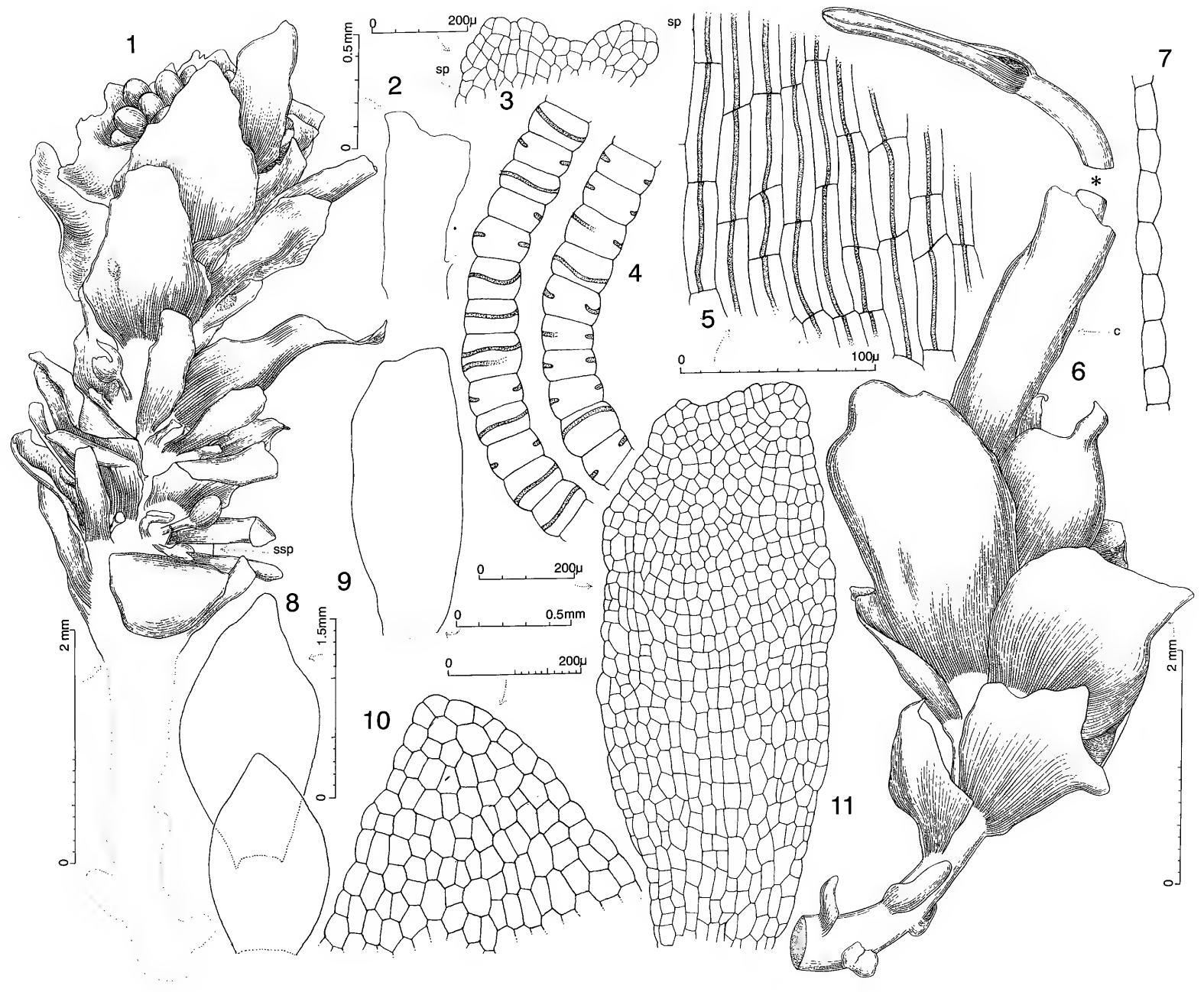

Fig. 5.
Haplomitrium minutum (E.O.Campb.) J.J.Engel & R.M.Schust. 1. Androecial plant; note position of antheridia and vertical stalked slime papillae (= ssp, at left of arrow). 2. Leaf from androecial shoot. 3. Apex of leaf from androecial shoot (sp = slime papilla). 4. Capsule wall, cross section (× 198). 5. Cells from median sector of capsule wall. 6. Plant with mature sporophyte; note true calyptra (= c). 7. Calyptra, cross section (× 198). 8. Subgynoecial leaves. 9. Leaf from gynoecial shoot. 10. Distal sector of subgynoecial leaf. 11. Leaf from gynoecial shoot, showing cellular detail. (All from isotype, MPN.)

Plants variable, the leafy shoots isophyllous or feebly anisophyllous (leaves of one row may be somewhat narrower), arising from a prostrate, branched, colorless rhizome; rhizomatous system covered by a mucilaginous sheath; leafy shoots erect, unbranched above, yellow-green to green, to 3 mm high. Leaves transversely inserted, ca. 1.4 mm wide, ca. 2 mm long (Campbell, 1987a) unistratose except for a 2(3)-stratose median-basal field, the shape variable (even on one shoot): often ovate to narrowly elliptic to linear or (occasionally) orbicular to subrhomboidal; apices narrowly rounded to bluntly acute to subacuminate, sometimes with a few sessile slime papillae; margins mostly entire, sporadically with 1–2 blunt teeth (margin then ± repand-dentate), the margins with a few sessile slime papillae; cells in median sector 24–36 × 38–55 μm; oil-bodies (Campbell, 1987a) mostly 11–21 per cell, finely granular, ellipsoidal, 2.6 × 4 μm.

Plants dioecious. Androecial plants with antheridia numerous in a terminal cluster or loosely scattered on stem: some axillary (and then up to 5 in an ill-defined zone and not restricted to bract axils), others freestanding; antheridia golden, the stalk massive, 6–8 cells high; axillary antheridia often accompanied by a slime cell at summit of a stalk of ca. 4 cells, other slime cells on a unicellular stalk and inconspicuous, the axillary antheridia occasionally also accompanied by narrowly attenuate scales. Gynoecial shoots (fertilized) with leaves abruptly enlarging toward summit, linear to narrowly ovate toward shoot base, the crowded bracts at summit of shoot a mixture of highly diverse shapes: innermost ones elongate-narrowly elliptical to lanceolate, these surrounded by a "rosette" of larger ones that are subrotund to broadly obovate but abruptly narrowing distally and forming a broadly apiculate to rounded projection; bract margins smooth, never repand-dentate. Sporophyte protective device a true calyptra, the calyptra translucent, smooth, unistratose (at least distally), the cells leptodermous.

Capsule oblong, the wall delicate, uniformly unistratose (except 2[?3]-stratose in apical area), 28–32 μm thick, formed of irregularly oriented (not tiered), oblong to linear cells usually with somewhat oblique end-walls, the cells with exceedingly thin, hyaline walls, in cross section cells convex on both free sides; cells 15–18 μm wide × 38–48 up to 64–72 μm long, each with a single (rarely two) longitudinal, brownish, narrow (2–2.4 μm wide) thickening band in form of an elongated complete ring, or sometimes incomplete at the ends.

Spores (23)26–32 μm, brown, the spore wall verruculate, the verruculae sparingly fused. Elaters 1-spiral, becoming bispiral at tips.

Distribution and Ecology: Known from only one source. Campbell (1987a) stated that it occurred as a weed in *Leptinella maniototo* turf at Cashmere Bowling Club's bowling green in Christchurch. Samples of that turf were grown in performance trial plots at the Turf Research Institute near Palmerston North. According to Campbell (1987a) the source of the *Leptinella* plants is likely to have been Dunback, Otago. David Havell (pers. comm., 2006) who worked with the *Leptinella* pot-trials at Palmerston North believes that the *Haplomitrium* occurred in pots of *Leptinella dioica* "Pahia form," a cultivar in widespread use for bowling greens, and that this form originates from Southland coastal turflands.

Order 2. **JUNGERMANNIALES** H.Klinggr.

Artificial key to genera of Jungermanniales of New Zealand[1]

General Key

1a. Vegetative gametophyte lacking recognizable leaves (but gametangial branches leafy) . . . . . Group A

1b. Vegetative plants bearing recognizable leaves 2

2a. Leaves varied in form but never clearly complicate-bilobed (abaxial face never ridged or winged) and never with a water-sac of ventral margin, or forming a ventral lobe 3

3a. Leaves with lamina absent or under 1 cell-tier high, divided to base into 2–4(6) uniseriate lobes; plants usually confervoid . . . . . Group B

3b. Leaves, lobed or unlobed, with distinct laminae, usually 2–many cells high (even when leaves are deeply lobed) 4

4a. Leaves of mature stems always (2)3–12(15)-lobed (never strictly bilobed), usually deeply so (if shallowly 3-lobed or -dentate, always strongly incubous) 5

5a. Rhizoids (usually frequent) scattered over ventral face of stem, or at ventral bases of leaves; underleaves 1–2-lobed, or lacking, lobes often ciliate. Leaves 2–3- or 3–4(5)-lobed only, always alternate; sexual branches never reduced and ventral-intercalary (exc. *Jackiella*). (*Lophozioideae*, *Plagiochilaceae* and *Acrobolbaceae*) . . . . . see Group H

5b. Rhizoids (often few or very local) only at bases of the distinct underleaves, or at bases of reduced appendages of stolons and/or flagella; underleaves often 3–4-lobed or more, lobes rarely ciliate, rarely reduced, then of 2 minute segments 6

6a. Vegetative (leafy) shoots, and/or flagelliform, microphyllous axes and/or sexual branches all, or in part, ventral-intercalary (at times such branches infrequent, but always present if searched for) . . . . . Group C

6b. Vegetative (leafy) shoots with branches all lateral (usually 1–2–3-pinnate, regularly or irregularly so); gametangia always on elongated leafy axes (acrogynous; acroandrous); geotropic, microphyllous, flagelliform branches never produced . . . . . Group D

4b. Leaves of mature shoots 0-lobed or 2-lobed (at most, isolated, 3-lobed leaves), the leaf margins entire or variously dentate/ciliate 7

[1]This key is adapted, with considerable modification, from Schuster (2000a). Extraterritorial genera that are known only from southern South America or the subantarctic islands are included, but placed in brackets, since a) all are included in various discussions within this flora, and b) a possibility exists that these genera eventually may be discovered in New Zealand.

7a. Leaf insertion (or at least orientation) clearly incubous. Underleaves nearly always distinct, large, as broad as stem or usually broader; rhizoids confined to fascicles from underleaf bases . . . . . Group E

7b. Leaf insertion (and orientation) transverse or succubous. Underleaves large to none; rhizoids scattered, or in fascicles from underleaf or leaf bases 8

8a. Isophyllous or subisophyllous: underleaves similar to lateral leaves in size and form. Usually erect in growth, with leaves transverse or ± incubous. Rhizoids usually in fascicles from underleaf bases . . . . . Group F

8b. Anisophyllous to distichous: underleaves lacking or differing in form and size from lateral leaves, at most 0.1–0.5 (rarely to 0.55) lateral leaves in area 9

9a. Rhizoids (usually readily located) clearly limited to ± sharply defined fields, at underleaf bases, or ventral lateral leaf bases (if scattered, leaves clearly opposed). Underleaves rarely wholly lacking; leaves alternate or opposed 10

10a. Underleaves distinct: usually at least 0.1–0.2 area of lateral leaves, most often bifid. Rhizoids always at underleaf (never leaf) bases; leaves usually alternate, opposite in some taxa . . . . . Group G

10b. Underleaves lacking (or mere minute, few-celled vestiges, at most minute lanceolate or subulate segments, the underleaves in a few taxa small and lamelliform, these then with free slime papilla formation). . . . . Group H

9b. Rhizoids (sometimes scarce) freely scattered (usually on normal, leafy stems), never fasciculate. Underleaves distinct varying to lacking; leaves clearly alternate 11

11a. Leaves vertically oriented; their insertion nearly transverse (no more than 5–15°) succubous, as regards dorsal half of insertion). Leaves usually shallowly to conspicuously bifid, rarely entire and unlobed. . . . . Group I

11b. Leaves clearly obliquely inserted and oriented, succubous, 0–2-lobed 12

12a. Leaves bilobed, shallowly to deeply so (sometimes with accessory teeth; rarely sporadic leaves trilobed) . . . . Group J

12b. Leaves unlobed, never bilobed in vegetative regions (but sometimes conspicuously ciliate) . . . . . Group K

2b. Leaves complicate-bilobed, the two lobes clearly folded over each other; or leaves, on ventral side, with a distinct water-sac or lobule (which is hidden from view, in

dorsal aspect of plant); the lobule reduced or vestigial in a few taxa (then leaves appearing simply incubously shingled) 13

13a. Underleaves of mature stems lacking; rhizoids scattered, or from lobule of leaf, or in small fascicles from stem (from loci where underleaf development was suppressed) . . . . . Group L

13b. Underleaves present, conspicuous; rhizoids always at bases of the underleaves, from stem or from underleaf base 14

14a. Underleaves unlobed, at most the apex toothed or lobulate . . . . . Group M

14b. Underleaves clearly bilobed or quadrilobed. 15

15a. Plants without water-sacs or lobules: leaves simply complicate-bilobed (the dorsal lobe usually slightly to clearly, sometimes greatly, smaller than the ventral). Leaf lobes usually variously dentate or ciliate; marsupium or coelocaule developed at apices of leading shoots; coelocaule at most with a reduced perianth at apex . . . . . Group N

15b. Plants developing distinct water-sacs (lobules), usually ± longer than broad, typically lying parallel to stem or weakly divergent 16

16a. Lobules of stem leaves (and/or branch leaves) galeate, or helmet-shaped, longer than wide, only feebly attached to (and often remote from) stem; water sac formed only by the inflated sac-like lobule. Plants usually deep- or brownish green, or tinted reddish to purplish (only *Lepidogyna* pale yellowish green). Branching smooth, without basal collar (except sometimes in *Frullania* spp.). . . . Group O

16b. Lobules (water sacs) of leaves formed by the infolded ventral lobe + opposed basal portion of the lobe, the lobules attached by an elongate keel to the lobe. Plants pale to yellowish to grass-green. Vegetative branches thecal, with a distinct basal sheath (except sometimes in *Nephelolejeunea*) . . . . . Group P

Group Keys

Group A. Mature vegetative plants essentially leafless and thalloid. Axis of 6 (or more) large cortical cell rows + many small inner cell rows; leaves reduced (to lateral 1- or 2-celled projections, each bearing a 1–2-celled papilla); rhizoids in fascicles from vestigial underleaves.

Only *Zoopsis* p. p. will key here.

Group B. Plants with leaves formed of 2–4 (wholly or largely) uniseriate, ciliiform lobes; disc lacking or less than 1 cell-row high.

Only *Telaranea* p. p. will key here.

Group C. Plants able to produce ventral-intercalary branches from axils of ± distinct underleaves (sometimes only ♂ and ♀ produced on ventral-intercalary branches). Plants usually

regularly with leaves (3)4–12-lobed (rarely only lobulate), whose margins may be dentate or ciliate. Ventral (less often lateral) branches flagelliform or stoloniform in many taxa. Rhizoids always from underleaf bases, sometimes local or rare. (Leaf insertion variable: incubous, succubous, or transverse.)

1a. Gametangia (♀, usually also ♂) all or mostly on ± abbreviated ventral-intercalary branches that mostly lack normal leaves; microphyllous flagelliform axes usually produced. (*Lepidoziaceae* + *Neogrolleaceae* + *Trichotemnomaceae*) 2
2a. Leaves all, or mostly, 3-lobed or -dentate, or shallowly 3–4-lobulate 3
3a. Leaves succubously inserted 1 oriented, of non-collenchymatous cells 4
4a. Cells large, leptodermous, smooth; with lateral-intercalary branches . . . . . *Paracromastigum* (p. 463) + *Hyalolepidozia* (p. 472)
4b. Cells small, verruculose, usually firm-walled; no lateral-intercalary branches 5
5a. Leaves deeply (2)3-fid, with long-acute lobes; underleaves deeply 2(3)-lobed . . . . . *Paracromastigum* (p. 463)
5b. Leaves shallowly, 3(4)-lobed, asymmetric; underleaves shallowly lobulate . . . . . *Chloranthelia* (p. 523)
3b. Leaves incubously inserted and oriented (if transverse, then irregularly 2–3–4-lobulate and cupped) 6
6a. Leaves transverse, hemispherically concave, apex irregularly (2)3–4-lobulate + dentate. Plants subisophyllous, the underleaves leaf-like; cells with coarse nodose trigones, the surface coarsely striate-papillose . . . . . *Neogrollea* (p. 102)
6b. Leave incubous (in *Acromastigum* in part, transverse; there 2–3-lobed or -lobulate at apex) 7
7a. Leaves 2–3-lobed for at least 0.5 their length, formed of rectangulate cells lacking trigones; lateral branching monopodial; plants subhyaline, pale green 8
8a. Cells firm-walled, small, lacking oil-bodies; lateral branches all intercalary; plants with a system of basal, creeping, small leaved or microphyllous rhizomatous or stoloniform axes . . . . . *Drucella* (p. 385)
8b. Cells thin-walled, large, with oil-bodies; lateral branches terminal, *Frullania* type; plants lacking basal rhizomatous or stoloniform axes . . . . . *Telaranea* (p. 270)
7b. Leaves shallowly (0)2–3-dentate or -lobulate. Branching pseudodichotomous (except *Bazzania exempta*); vigorous terminal branches laterally displacing main stem. Copious ventral flagella but lateral branches never flagelliform. . . . . *Bazzania* (p. 415)
2b. Leaves (at least of mature stems) all, or predominantly (rarely only in part), 4 or more -lobed or -lobulate 9
9a. Leaves clearly incubously inserted and oriented 10
10a. Plants not dendritic, without a creeping caudex; lateral (vegetative) branches normally all *Frullania* type 11
11a. Leaves (3)4–6(7)-lobed 12
12a. Leaves (more or less) strongly asymmetrical, with dorsal sector

larger than ventral; disc usually as high, or higher than lobes; cells firm-walled, ± opaque; stem lacking a conspicuous hyaloderm . . . . . *Lepidozia* (p. 195)

12b. Leaves ± symmetrical; disc usually under 0.5 height of leaf; cells thin-walled, ± rectangulate; stem with hyaloderm distinct . . . . . *Telaranea* (p. 270)

11b. Leaves (7)8–12(13)-lobed. Otherwise as in *Telaranea* but lacking a hyaloderm . . . . . *Telaranea* (p. p., *T. pulcherrima*) (p. 319)

10b. Plants dendritic: a copiously branched erect shoot arising from a caudex, which freely produces geotropic flagelliform axes; lateral branches of *Frullania* + *Microlepidozia* types . . . . . *Megalembidium* (p. 525)

9b. Leaves transverse or subtransverse to succubous in insertion and orientation 13

13a. Leaves with lobes unarmed (except sporadically at base); cells lacking trigones; plants with perianths, a marsupium lacking 14

14a. Leaves (5)6–8-lobed, each lobe ending in a hyaline, erect, finger-like cell. Oil-bodies absent; disc cells small, thick-walled; lateral branches all of *Frullania* type . . . . . *Psiloclada* (p. 381)

14b. Leaves 3–4(5–6)-lobed, lobes never ending in elongated, erect, hyaline cells 15

15a. *Microlepidozia*-type branching present; plants opaque, firm, dull green to fuscous; cells small, firm-walled . . . . *Kurzia* (p. 358)

15b. *Microlepidozia*-type branching lacking; plants usually subhyaline, pale to whitish green 16

16a. Leaves strongly asymmetrical, shallowly (3)4–5-lobed, dorsal lobe smaller; surface conspicuously papillose . . . . . *Chloranthelia* (p. 523)

16b. Leaves symmetrically (3)4–6-lobed; surface smooth or slightly roughened or striolate . . . . . *Pseudocephalozia* (p. 457)

13b. Leaves with lobes and disc copiously armed with pluricellular cilia/laciniae; cells with coarse trigones; plants with marsupia, a perianth lacking. Leaves asymmetrically 4-lobed, the dorsal lobe smaller . . . . . *Trichotemnoma* (p. 543)

1b. Gametangia produced on leafy, elongated or leading shoots (♂ usually becoming intercalary; ♀ sometimes or often innovating if unfertilized). Microphyllous geotropic axes absent or present. (Plants usually tristichous, often ± isophyllous.) 17

17a. Leaves deeply bisbifid (sporadically trifid) for 0.5–0.85 their length, the lateral sinuses clearly shallower. Cells equally firm-walled 18

18a. Leaves thin, unistratose; terminal branches present 19

19a. Plants pale green; bracteolar antheridia present; perianth absent, a coelocaule present. Southern South America . . . . . [*Vetaforma*]

19b. Plants brown to fuscous; bracteolar antheridia lacking; perianth conspicuous, a coelocaule absent. Branching malleable: *Acromastigum-Microlepidozia-Frullania*-type terminal + intercalary branches. Capsule wall 4–5-layered. Southern South America . . . . . [*Pseudolepicolea*]

18b. Leaves rigid, horny, polystratose; terminal branches lacking. Plants often blackish. Southern South America . . . . . [*Herzogiaria*]

17b. Leaves (2-), 3- or 4-fid, the sinuses all about equal in depth 20
20a. Leaves usually over 0.5 (3)4-lobed, transverse to strongly succubous (if transverse, then with lobes ciliate and/or ending in setaceous lobes); leaves, if asymmetric, with dorsal lobe smaller. Plants lacking geotropic stolons; perianth conspicuous, androecial bracteoles lacking antheridia 21
21a. Leaf cells thin-walled or equally firm-walled, roughened. Elaters with 2 narrow spirals 22
22a. Perianth mouth wide open; leaves (at least near gynoecia) with opposed teeth and/or cilia . . . . . *Temnoma* (p. 147)
22b. Perianth mouth strongly contracted; leaf (+ underleaf and bract) margins edentate/eciliate (at most 1 tooth of disc). Southern South America . . . . . [*Archaeochaete*]
21b. Leaf cells with walls thin, the angles forming conspicuous trigones. Leaf lobes setaceous, rigid; perianth contracted to mouth; elaters 1-spiraled, the spiral broad . . . . . *Archeophylla* (p. 165)
20b. Leaves usually under 0.35 2–3–4-lobed (or leaves incubous), the lobes/margins entire to toothed with broad-based teeth, never ciliate; leaves often asymmetric, then with larger dorsal lobe 23
23a. Lateral branches all axillary, intercalary (rare exceptions aside); perianth conspicuous, long-emergent; ventral-intercalary stoloniform axes common; leaf cells shorter, the length:width under 2:1 . . . . . *Triandrophyllum* (p. 115)
23b. Lateral branches of *Frullania* type; perianth vestigial, an *Isotachis*-type rigid perigynium present; ventral stolons usually lacking; leaf cells elongated 24
24a. Non-julaceous; shoot tips usually cernuous; leaf cells under 4–5:1 . . . . . *Isotachis* (vol. 2)
24b. Julaceous, fragile, leaves very flimsy; shoot tips erect; leaf cells to 8–10:1 . . . . . *Eoisotachis* (vol. 2)

Group D. Plants unable to form ventral-intercalary branches; both vegetative and gametangial axes lateral in origin (very rarely from terminal-ventral branches); plants predominantly, often regularly, 1–2- to 3–4-pinnately branched. Leaves variable; 3- or 4-lobed, sometimes bisbifid; never 5-lobed or more, sometimes strongly asymmetric; never forming geotropic, microphyllous stolons or flagella. Plants isophyllous to anisophyllous.

1a. Leaf margins never armed with hyaline, rigid, thick-walled 1-celled setae/cilia 2
2a. Leaves transverse to succubous, never bisbifid, symmetric or subsymmetric, copiously armed with or dissolved into cilia; cells rectangulate in lamina, often tiered, lacking trigones, the surface ± roughened 3
3a. Perianth present; branching irregularly and usually sparing 4
4a. Perianth conspicuous, ± emergent; plants deep green to brown or fuscous 5
5a. Leaf lobes caudate, the margins copiously armed with pairs of opposing cilia, the cilia repeatedly dichotomously branched; ventral-intercalary type branching lacking . . . . . *Castanoclobos* (p. 168)

5b. Leaf lobes acute to lanceolate, the margins entire or with opposed spinescent teeth or cilia, the armature normally unbranched; ventral-intercalary type branching typically present . . . . . see *Temnoma* (p. 147)

4b. Perianth a low cap or urn, at summit of a distinct coelocaule; plants yellow-green. Never with ventral-intercalary branches . . . . . *Leiomitra* (p. 173)

3b. Perianth lacking, a clavate, hispid coelocaule developed; branching ± regularly 1–3(4)-pinnate. Plants pale or yellow-green 6

6a. Branching usually 2–3(4)-pinnate, the branches never tapered, not cernuous; plants vigorous, prostrate to pendulous; *Acromastigum*-type branching never present . . . . . *Trichocolea* (p. 179)

6b. Branching 1-pinnate (primary pinnae very rarely with a short secondary branch), the pinnae tapered, often flagelliform, often cernuous; plants small (to 1 cm tall), erect or suberect; *Acromastigum*-type branches rare . . . . . *Eotrichocolea* (p. 191)

2b. Leaves somewhat to clearly incubous in insertion and/or orientation; cells not clearly rectangulate, never tiered, with walls firm (with coalescent trigones) or thin (with coarse, nodose trigones), the surface smooth 7

7a. Leaves symmetrically or subsymmetrically bisbifid, the lobes lanceolate to long-acuminate, entire or sporadically ciliate; plants greyish; perianth absent, a clavate, hispid coelocaule present . . . . . *Lepicolea* (p. 95)

7b. Leaves 3–4(5)-lobed, usually asymmetric (dorsal lobe largest); lobes triangular, rarely lanceolate, never acuminate, usually toothed and/or ciliate; plants brown to red-brown; perianth present, a coelocaule not developed 8

8a. Lateral branches attenuate, becoming flagelliform; gynoecia all terminating weak lateral branches. Stem underleaves quadrifid; shoots strongly complanate, lax, often pendulous . . . . . *Dendromastigophora* (vol. 2)

8b. Lateral branches never attenuate and flagelliform; gynoecia terminating main axes . . . . . *Ptilidium* (vol. 2)

1b. Leaf margins armed with stiff, hyaline, 1-celled setae. Leaves asymmetric, succubous 9

9a. Branching regularly 1–2(3)-pinnate, the branches freely developed; ultimate branches with leaves + underleaves fused in distinct rings; plants never gemmiparous . . . . . *Herzogianthus* (vol. 2)

9b. Branching irregular, the branches sparing; both main axes and branches with leaves and underleaves free; plants with reddish brown stellate gemmae developed at shoot apices . . . . . *Chaetophyllopsis* (vol. 2)

Group E. Plants with leaves incubously oriented (and insertion usually at least weakly incubous), usually bilobed or bidentate (rarely unlobed). Rhizoids limited to bases of underleaves and/or geotropic stolons.

1a. Leaves never vittate, 0.05–0.55 bilobed (less often unlobed or 2–3-lobulate or 2–4-denticulate at apex); lobes, if distinct, never lanceolate and/or acuminate. Perianth bluntly trigonous, or lacking 2

2a. Geotropic, rhizoidous stolons and/or flagella lacking 3

3a. Branching all or mostly ventral-intercalary; gynoecia and androecia on short, ventral-intercalary branches; leaves unlobed, apices entire or bidentate . . . . . *Calypogeia* (p. 533)

3b. Branches normally lateral-terminal, *Frullania* type; gynoecia and androecia on leading leafy shoots; leaves irregularly lobulate. Southern South America . . . . . [*Xenocephalozia*]

2b. Geotropic rhizoidous stolons and/or flagella usually frequent 4

4a. Vegetative branches all lateral-intercalary. Leaves lepidozioid, usually 2(3)-lobed, few-celled; underleaves similar, usually smaller . . . . . *Hyalolepidozia* (p. 472)

4b. Vegetative branches not lateral-intercalary 5

5a. Leaves without a field of large, inflated basal cells; leaves not canaliculated 6

6a. *Frullania*-type terminal branching abundant; branching usually dichotomous. Caudex lacking 7

7a. Stolons all axillary from underleaf axils; stem without hyaloderm, with thick-walled cortical cells in numerous rows; leaves (often obscurely) (2)3-dentate . . . . . *Bazzania* (p. 415)

7b. Stolons all or many terminal, not axillary; stem with a firm hyaloderm, the cortical cells in 7 rows, at least on branches; leaves 0–2-lobed . . . . . *Acromastigum* (p. 390)

6b. *Frullania*-type lateral branches (usually) lacking; branching never pseudodichotomous. Leafy shoots unbranched or almost unbranched, arising from a caudex or bearing stolons 8

8a. Leaves planodistichous, unlobed or bidentate at apex. Leafy shoots giving rise to ventral-intercalary, geotropic flagelliform axes; leaf apex entire . . . . . *Mnioloma* (p. 537)

8b. Leaves concave, 2–3-lobed; leafy shoots giving rise to geotropic flagelliform axes . . . . . see *Isotachis* (vol. 2)

5b. Leaves with a distinct field of elongated, thin-walled ± inflated basal cells (in contrast to the small, firm-walled isodiametric distal cells); leaves strongly canaliculate. Leaf apices minutely (2)4-dentate . . . . . *Lembidium* (p. 503)

1b. Leaves vittate, 0.55–0.85(09) bifid, the vitta of elongate cells extended into each lobe; leaves often falcate-lobed, the lobes lanceolate to acuminate. Perianth fusiform, bluntly triplicate, mouth deeply 6-lobed . . . . . *Herbertus* (p. 108)

Group F. Plants usually erect or stiffly ascending, isophyllous or weakly anisophyllous; underleaves over 0.7 area of lateral leaves, usually similar in form, both unlobed or 2(3)-lobed or -dentate. Rhizoids only at underleaf bases (except *Anthelia*, p. p.). Leaves and underleaves mostly unlobed and edentate, sometimes bilobed. Plants either pigment-free, brownish, or fuscous; never reddish. Asexual reproduction uniformly lacking. (All on soil or rocks.)

1a. Leaves 1-layered, mostly ± translucent 2

2a. Cells with coarse nodular or lobed trigones, large (35–40 μm wide in middle). Leaves shallowly (under 0.25) 2–3–4-dentate or -lobulate; underleaves identical, unlobed, retuse or lobulate. (If leaves and underleaves unlobed, stiffly spreading, see *Acromastigum*.) 3

3a. Leaves 2(3)-lobulate; underleaves spoon-shaped, unlobed; ♂ and ♀ gametangia on leading leafy axes; branches only lateral-intercalary; surface smooth. Southern South America . . . . . [*Pleurocladopsis*]

3b. Leaves variably 3–4-lobulate + dentate distally; underleaves similar; both almost hemispherical; ♂ and ♀ gametangia on short, axillary branches; branching malleable, ventral- + lateral-terminal + intercalary; surface strongly striate-papillose . . . . . *Neogrollea* (p. 102)

2b. Cells thin- to firm-walled, at most with large but concave-sided trigones, smaller (median under 34 μm wide) 4

4a. Leaves and underleaves lobed, even if very shallowly so 5

5a. Leaves (isolated exceptions aside) bilobed or bidentate; wall pigments absent, or brown to reddish brown; cells never strongly elongated 6

6a. Leaf with surface covered by large, hyaline, dome-shaped thickenings over cell wall intersections (not over lumina). Plants tiny, pale or whitish green, with spreading leaves and underleaves at most subcontiguous; rhizoids at underleaf bases only; branches freely terminal, *Frullania* type; perianth trigonous. Southern South America . . . . . [*Pigafettoa*]

6b. Leaves smooth or minutely papillose. Leaves contiguous or imbricate (stem usually hidden), erect or suberect 7

7a. Lateral leafy branches normally terminal, of *Frullania* type; oil-bodies lacking 8

8a. Leaves and underleaves identical, both over 0.55 bifid, with smooth margins; ♂ and ♀ gametangia on leading axes (ours paroecious); leaves with age often becoming decolorate and whitish . . . . . *Anthelia* (p. 547)

8b. Leaves 2(3)-fid, underleaves bifid, to 0.35, the margins ± denticulate; ♂ and ♀ on short ventral-intercalary branches (dioecious); leaves not becoming decolorate and whitish . . . . . *Chloranthelia* (p. 523)

7b. Leafy branches normally intercalary, oil-bodies present (known only for *Isophyllaria*) 9

9a. Leaves cuneiform, transverse to weakly succubous, bifid to 0.5–0.75, the lobes abaxially canaliculated below; perianth present, conspicuous; capsule wall 3–4-stratose; terminal branches sometimes present, at times frequent . . . . . *Isophyllaria* (p. 141)

9b. Leaves oblong-ovate (at times narrowly so), transverse to weakly incubous, bifid to 0.35–0.5, the lobes plane; perianth lacking, the innermost gyre of large bracts + bracteole appressed to calyptra; capsule wall 2-stratose; terminal branches lacking. Southern South America . . . . . [*Grollea*]

5b. Leaves ± oblong, variably and shallowly 2–3–4-lobed; underleaves similar but 2-lobed; fuscous; cells strongly elongated, thin-walled, to 8–10:1 basally. Plants julaceous subaquatic, lax . . . . . *Eoisotachis* (vol. 2)

4b. Leaves and underleaves ± ovate-rectangular to spoon-shaped to orbicular-ovate, broad-based, quite unlobed. Branching uniformly axillary, intercalary 10

10a. Plants filiform, with remote ovate-triangular leaves and, optimally similar, ± triangular underleaves; rhizoids scattered; no stolons. All branches lateral-intercalary. Prince Edward Is. . . . . [*Invisocaulis*]

10b. Medium-sized, with contiguous to imbricate, ovate-orbicular leaves and underleaves; rhizoids at underleaf bases; with stolons. Some ventral-intercalary branches . . . . . *Hygrolembidium* p. p. (subg. *Hygrobiellopsis*) (p. 511)

1b. Leaves firm to rigid, polystratose (at least in largest part), opaque. Leaves unlobed (or, sporadically, to 0.2–0.25 bilobed); plants stoloniferous 11

11a. Plants bright green; ♂ and ♀ gametangia on short, leafless intercalary branches; leaves never stiffly spreading, basally strongly concave 12

12a. Branching exclusively intercalary, lateral and ventral; cells, all or most, lacking oil-bodies; stem with hyaloderm lacking; leaves not cucullate . . . . . *Hygrolembidium* (p. 509)

12b. Branching frequently terminal; cells with oil-bodies; stem with a hyaloderm surrounding smaller, firm-walled intracortical cells; leaves cucullate . . . . . *Isolembidium* (p. 499)

11b. Plants deep green to olive-green to almost black; gametangia on ± elongated, leafy axes; leaves rigid, ± spreading, not or little concave . . . . . *Pachyglossa* (vol. 2)

Group G. Plants anisophyllous to almost distichous, with leaves alternate to (at most) subopposite, succubous or transverse, 0–2-lobed (rarely 2[3]-lobed). Underleaves usually under 0.5 (rarely 0.5–0.6) leaves in area (if, rarely, larger, very different from leaves in shape). Rhizoids in fascicles: from bases of underleaves, never scattered (except in a few taxa with sharply opposed leaves). (An artificial group, including taxa of *Lepidoziaceae*, *Geocalycaceae*, *Lophocoleaceae*, *Jungermanniaceae*.)

1a. Stem, in cross section, with a conspicuous hyaloderm (medullary cells usually distinct by transmitted light as an opaque central strand); cortical cells 1.5–4× medullary in diam. or even larger 2

2a. Leaves subhorizontally or obliquely oriented; cells large, hyaline, leptodermous; hyaloderm very conspicuous; underleaves reduced, under 0.2 area of leaves, few-celled, bifid. Leaves with a symmetrically bilobed, rectangulate lamina, 4 or more cells broad, conspicuously bifid (*Lepidoziaceae*) 3

3a. Terminal branches lacking, the lateral branches all intercalary . . . . . see *Hyalolepidozia* (p. 472)

3b. Terminal, *Frullania*-type branches present, common 4

4a. Leaves with lobe apices sharp, persistent; sinuses descending under 0.25 leaf length . . . . . *Zoopsidella* (p. 495)

4b. Leaves with long-tapered apices, of moniliform cells, fragmenting; sinus descending over 0.25 leaf length . . . . *Zoopsis* p. p. (*Z. ceratophylla*) (p. 484)

2b. Leaves transverse or almost so, vertically oriented; cells firm, small, with ± distinct trigones; hyaloderm poorly demarcated, the enlarged cortical cells thick-walled; underleaves to 0.5(0.65) area of leaves 5

5a. Leaves entire or shallowly 2(3)-lobed/lobulate, their surfaces smooth; ventral-terminal branches present . . . . . *Acromastigum* (p. 390)

5b. Leaves to 0.5 2(3)-fid, covered by coarse, convex, lenticular thickenings over cell wall intersections; ventral branches only intercalary. Southern South America . . . . . [*Pigafettoa*]

1b. Stem without a perceptible hyalodermis; cortical cells thin- or firm-walled, never conspicuously larger than intracortical in cross section 6

6a. Ventral-intercalary microphyllous stoloniform axes absent. *Acromastigum*-type branching absent; plants usually large, with collenchymatous leaf cells; leaves 0–2-lobed and underleaves 0–2-lobed, or with lateral teeth or laciniae large enough to simulate lobes 7

7a. Leaves opposed or almost opposed, the dorsal bases usually contiguous or connate. Underleaves bifid. (*Lophocoleaceae*, *Geocalycaceae*) 8

8a. Perianth conspicuous; no marsupium; surface smooth or with solitary papillae (plants never conspicuously dull when dry) 9

9a. Plants whitish to pure green; perianth trigonous . . . . . *Chiloscyphus* (p. p.) (vol. 2)

9b. Plants brown to fuscous; perianth bilabiate, laterally compressed at least above . . . . . *Leptoscyphus* (p. p.) (vol. 2)

8b. Perianth lacking; a marsupium developed; surface densely covered by papillae (plants diagnostically dull when dry) . . . . . *Saccogynidium* (vol. 2)

7b. Leaves obviously alternate, the dorsal leaf bases not juxtaposed, never connate 10

10a. Asexual reproduction lacking, or via gemmae, or via caducous leaves, cells with few (under 12) oil-bodies (the oil-bodies at times botryoidal) 11

11a. Plants with leaves ± constricted at base, freely caducous, the mature plants extensively denuded. Plants brownish; perianth laterally compressed at the closed mouth; branching mostly intercalary; leaves ± obdeltoid or obovate. Southern South America . . . . . [*Anomylia*]

11b. Plants with leaves broad-based, persistent, the shoots never denuded 12

12a. Plants strongly laterally compressed, with broadly rounded leaves. Underleaves free, minute, divided to near base into 2–3 linear segments, the flanks unarmed; perianth 2-lipped, compressed; rhizoids in part scattered. Southern South America . . . . . [*Pedinophyllopsis*]

12b. Plants never laterally compressed, usually dorsiventrally ± flattened, or with vertical leaves 13

13a. Perianth 2-lipped, laterally compressed at least above (with broad, bilobed and/or toothed lateral faces, the ventral, third lobe, narrowed, usually abbreviated, often infolded) 14

14a. Leaves 1-stratose throughout; dorsal-intercalary branching never present; underleaves broader than stem, the lamina margins usually conspicuously armed 15

15a. Plants green, chiloscyphoid; perianth with longi-

tudinal, ± undulate, toothed wings, in addition to the 3 major keels . . . . . *Lamellocolea* (vol. 2)

15b. Plants brown to fuscous; perianth surfaces unarmed (at most keels ± winged) . . . . . *Leptoscyphus* (vol. 2)

14b. Leaves, except marginally, 2–3-stratose; dorsal-intercalary branching (*Andrewsianthus*-type) present; underleaves narrower than stem, small, the lamina margins entire or with 1(3) small teeth. Leaves unlobed, entire. Southern South America . . . . . [*Evansianthus*]

13b. Perianth symmetrically 3-sided (ventral face as broad as lateral faces) or inflated and unkeeled, the mouth equally 3-lobed (each lobe often again bilobed). 16

16a. Leaves ± flat or at least the dorsal margin ± (often feebly) decurved. ♀ Bracts and bracteoles equal or subequal; plants sometimes gemmiparous 17

17a. Gametangial branches all highly reduced; both ♂ and ♀ branches short, the ♂ spicate, compact. Cells typically with coarse, often nodose trigones . . *Heteroscyphus* (?incl. *Amphilophocolea*) (vol. 2)

17b. Gametangial branches unspecialized; androecia and gynoecia on (usually) elongated, or if short, leafy branches. Cells with usually thin walls, with small or very small trigones. . . . . *Chiloscyphus* (vol. 2)

16b. Leaves ± concave, often strongly so, the dorsal margin mostly ± incurved; plants never gemmiparous 18

18a. Leaf insertion, including at dorsal end, clearly succubous, leaves obliquely oriented (concavity turned up, or toward shoot apex); leaves usually decurrent dorsally; ♀ bracteole usually smaller than bracts; perianth usually inflated, convex-sided . . . . . *Clasmatocolea* (vol. 2)

18b. Leaf insertion dorsally transverse or feebly incubous, the leaves incubously oriented (concavity turned ± toward ventral face of plant); leaves nondecurrent; ♀ bracteole subequal to bracts in size, obovate, large; perianth faces flat or concave. Southern South America . . . . . [*Xenocephalozia*]

10b. Asexual reproduction via caducous or fragmenting teeth of distal portions of the bilobed leaves; cells leptodermous, each with numerous (20–40 or more) minute, finely papillose oil-bodies. Leaves flat, neither with convex

dorsal margin, nor concave, even basally; plants maximally flattened, delicate, fragile; *Frullania*-type branches freely formed; usually sterile . . . . . *Leptophyllopsis* (vol. 2)

6b. Ventral- and/or lateral-intercalary, microphyllous-rhizoidous, usually strongly geotropic branches freely developed (often axillary from lower leaves or leafy shoots) and/or with a creeping, rhizoidous caudex 19

19a. Leaves deeply (usually 0.3–0.65 or more) 2- or 2–3-fid, formed of ± elongated, thin- or equally firm-walled, trigone-free cells; underleaves 2-, 2–3-, or 3-fid; *Acromastigum*-type branches usually present . . . . . *Paracromastigum* (p. 463)

19b. Leaves unlobed (rarely retuse or emarginate), entire-margined or 2- to 3–4-denticulate at apices; *Acromastigum*-branches absent 20

20a. Leaves, except in marginal/peripheral sectors, polystratose, firm, unlobed (or retuse); underleaves unlobed, usually ± denticulate; leaves strongly concave; branches all intercalary 21

21a. Leaves succubous, never fleshy; dorsal-intercalary branches present, from dorsal end of leaf axils; plants closely prostrate. Southern South America . . . . . [*Evansianthus*]

21b. Leaves vertical, transverse or weakly succubous, fleshy; dorsal-intercalary branches lacking, the lateral branches clearly axillary in leaves; plants erect in growth . . . . . *Hygrolembidium* (p. 509)

20b. Leaves uniformly 1-stratose 22

22a. Rhizoids purplish. Plants chestnut-brown, branching typically all ventral-intercalary, leaves polished and nitid, strongly dorsally assurgent . . . . . *Acroscyphella* (vol. 2)

22b. Rhizoids colorless 23

23a. Leaves concave or navicullariform 24

24a. Leaves clearly to closely imbricate, hiding stem from view, elongated, shallowly 2(3)-lobed or 2–4-denticulate at apex, vertical, transversely inserted at dorsal ends; leaves with median-basal or at least basal cells conspicuously larger; oil-bodies lacking 25

25a. Leaves spreading, navicullariform, the shoot complanate; leaf tips narrowly 2–4-lobulate/dentate . . . . . *Lembidium* (p. 503)

25b. Leaves suberect, closely imbricate, the shoot (more or less) julaceous; leaf apices shallowly 2(3)-lobed, with broad sinuses . . . . . *Chloranthelia* (p. 523)

24b. Leaves remote or contiguous, saucer-shaped, strongly concave, rounded, unlobed, subvertical, dorsal insertion ends oblique; leaves lacking an area of enlarged cells in basal sector; oil-bodies (1)2–3 in some/many cells. Underleaves very inconspicuous, appressed to stem . . . . . *Hepatostolonophora* (vol. 2)

23b. Leaves chiloscyphoid, with deflexed dorsal leaf margins, the leaves not adaxially concave . . . . . *Stolonivector* (vol. 2)

Group H. Plants like those of Group G, but essentially distichous; ventral merophytes narrow, underleaf-free, or with minute, subulate vestiges, or—at most—small lamellae with many small cilia or papillae. Leaves alternate or exactly opposed, unlobed, or 2– 4-lobed, entire-margined or variously toothed and/or ciliate. Rhizoids either at the bases of the underleaf vestiges or at ventral leaf bases, almost never scattered (or leaves 3–4-lobed). (Artificial group including taxa of *Lophozioideae*, *Plagiochilaceae*, *Jackiellaceae*, *Acrobolbaceae*, *Lophocoleaceae*.)

1a. Leaves clearly alternate, their dorsal bases never juxtaposed 2

2a. Stem without a hyalodermis. Leaf cells usually ± clearly collenchymatous, with coarse trigones, with 1–few, large granular oil-bodies per cell; rhizoids scattered or often in fascicles at ventral leaf bases 3

3a. Perianth lacking, a pendent marsupium developed at apices of leading or (*Jackiella*) ventral-intercalary branches 4

4a. Leaf insertions not extending to stem midline dorsally, a leaf-free strip present; plants usually deep brown to fuscous; ♂ and ♀ on short ventral-intercalary branches lacking normal leaves . . . . . *Jackiella* (p. 634)

4b. Leaf insertions extending to stem midline dorsally, a leaf-free strip lacking; plants lacking secondary pigments or, if present, then reddish or purplish or (*Austrolophozia*) with distal parts of leaves in sun reddish brown or golden brown; ♂ and ♀ on leading shoots 5

5a. Secondary pigments lacking; leaf surface conspicuously papillose (smooth in *A. concinnus*); rhizoids often confined to ventral base of leaves, not forming a ventral mat; ♂ bracts moderately concave to ventricose at base, the antheridia covered by the bracts . . . . . *Acrobolbus* (vol. 2)

5b. Secondary pigments present, reddish or purple brown or (*Austrolophozia*) tinged with reddish brown or golden brown in distal parts of leaves; leaf surface (lamina) smooth; rhizoids in a dense ventral mat forming a decurrent bundle; ♂ bracts leaf-like, the antheridia exposed 6

6a. Leaves unlobed; plants with reddish or purple-brown pigments; gemmae lacking; marsupium very long and slender, buried in substrate . . . . . *Goebelobryum* (vol. 2)

6b. Leaves (2)3–4(5)-lobed; plants in sun with reddish brown or golden brown pigments in distal parts of leaves; gemmae present; marsupium conoidal, elevated above substrate . . . . . *Austrolophozia* (vol. 2)

3b. Perianth distinct, inflated-plicate or inflated-trigonous or ± laterally compressed, then wide at mouth, the plants never with a marsupium 7

7a. Perianths broadly 2-lipped, laterally sharply compressed, without a ventral (third) face (*Plagiochilaceae*) 8

8a. Vegetative branches lateral-intercalary and/or of *Frullania* type, never ventral-intercalary . . . . . *Plagiochila* (vol. 2)

8b. Vegetative branches all ventral-intercalary, never lateral-intercalary. Leaves ± erect, laterally appressed . . . . . *Acrochila* (vol. 2)

7b. Perianth inflated and ± contracted to mouth, or trigonous to urceolate and wide at mouth, never 2-lipped. Gynoecia always with a ± reduced bracteole 9

9a. Rhizoids (sometimes infrequent) always scattered; perianth inflated, plicate, ± narrowed to mouth; asexual reproduction common 10

10a. Leaves (in ours) 2–3-lobed, the 2–3-lobed leaves in about equal frequency, the lobing at times asymmetric, the dorsal-most lobe smaller and shorter; ventral leaf base entire, without cilia; underleaves lacking . . . . . *Tritomaria* (p. 666)

10b. Leaves ± symmetrically (3)4-lobed; ventral leaf base with 1–several cilia; underleaves distinct. Southern South America . . . . . [*Lophozia* (subg. *Barbilophozia*, *Orthocaulis*)]

9b. Rhizoids frequent, in fascicles at bases of reduced or minute underleaves; perianth wide at mouth, 3-lobed (ventral lobe sometimes narrower); asexual reproduction absent 11

11a. Leaves mostly convex, 2(3)-dentate at apex, their insertion lines not attaining dorsal stem midline (with a "leaf-free" strip); perianth with third, ventral face narrow. Plants strongly dorsiventrally flattened . . . . . *Pseudolophocolea* (vol. 2)

11b. Leaves concave, often strongly so, usually unlobed or edentate, sometimes pluridentate, the insertion dorsally attaining stem midline; perianth trigonous or inflated, the ventral face not or little narrowed . . . . . *Clasmatocolea* (p. p.) (vol. 2)

2b. Stem with a ± distinct hyalodermis . . . . . see Group G

1b. Leaves perfectly opposed in pairs, their dorsal bases juxtaposed or ± connate 12

12a. Perianth sharply laterally compressed; ♀ bracts free from bracteole, leaf-like; plants usually brownish . . . . . *Plagiochilion* (vol. 2)

12b. Perianth not or weakly laterally compressed, contracted to mouth; ♀ bracts + bracteole united, often forming a sheath; plants often purplish or reddish, or reddish brown 13

13a. Leaves erect-appressed, reniform-orbicular, the plant strongly laterally compressed; branching mostly lateral (intercalary + *Frullania* type), rarely ventral-intercalary. Cortical cells, like medullary, thin-walled. Southern South America . . . . . [*Protosyzygiella*]

13b. Leaves loosely to strongly laterally patent, plants not laterally compressed; branches all or predominantly ventral-intercalary. Cortex 1–3-stratose, of thick-walled cells. [Kerguelen] . . . . . [*Syzygiella*]

Group I. Plants with leaves transversely oriented (vertical), always alternate, usually bilobed (less often unlobed), the dorsal half of insertion lines within 5° of being transverse (sometimes decurrent). Underleaves usually very small (under 0.3 leaf area) or none. Perianths distinct (except in *Gymnomitrion*); cells with oil-bodies (except in *Metahygrobiella*, which lacks stolons).

1a. Leaves bilobed (rarely only emarginate), never hyaline-margined, the margins entire; shoots not filiform-julaceous (except *Cephalomitrion*) 2

2a. Leaves remote to contiguous to imbricate, never tightly appressed; leaf perimeters, *in situ*, easily evident; shoots not filiform-julaceous. Cells never armed with high lenticular papillae 3

3a. Leaves clearly bifid, the transverse dorsal ends interlocking; perianths included, short, or lacking. Plants freely stoloniferous; cells with 2–3 granular oil-bodies. (*Gymnomitriaceae*, p. p.; all alpine) 4

4a. Perianth well developed, sheathed closely by the erect bracts, without a perigynium at its base; plants procumbent, with stiffly spreading leaves with abaxially sulcate lobes; surface coarsely papillose. Autoecious . . . . . *Acrolophozia* (p. 785)

4b. Perianth absent or a short tube hidden within the erect bracts; plants erect (ours usually fuscous to piceous), with leaf lobes not abaxially sulcate; surface smooth or weakly papillose. Leaves with margins flat or nearly so; branches all from middle or lower ends of leaf axils; gynoecium with a low perianth + distinct perigynium . . . . . *Marsupella* (p. 798)

3b. Leaves, usually bifid or bilobed, with dorsal insertion lines extending to, but not beyond, stem midline; perianth free, conspicuous, externally evident 5

5a. Stem lacking a hyaloderm; cortical cells usually firm-walled, no larger than medullary; cells with oil-bodies present 6

6a. Cells minute or very small (usually 9–18 μm broad), usually thick-walled and lacking trigones; plants small or minute, with small, usually remote leaves. Terminal branches absent or rare 7

7a. Underleaves distinct, to 0.5 area of lateral leaves; perianth bluntly trigonous; gemmae lacking. Seta with 8+4 cell rows; otherwise *Cephaloziella*-like. Southern South America . . . [*Amphicephalozia*]

7b. Underleaves lacking or very small (rarely larger in *Cephaloziella*; this with a 4+4-seriate seta); perianth 4–5-plicate or at apex of a perigynium; gemmae present, 2-celled, elliptical (but infrequent or lacking in most species of *Allisoniella*). Seta of the 4+4 or 8+4 type 8

8a. Leafy stems ± procumbent, not arising from a caudex, leaf lobes 2–9(12) cells broad; minute plants, with non-sulcate leaf lobes; seta with 4+4 cell rows . . . . . *Cephaloziella* (p. 578)

8b. Leafy stems erect, arising from an extensive caudex; leaf lobes 15–25 cells wide, usually abaxially sulcate; small but not minute, fuscous or purplish plants, with rigid stems; seta of the 8+4–12 type . . . . . *Allisoniella* (p. 570)

6b. Cells larger: normally 17–35 μm wide or more in leaf middle, usually with conspicuous or nodose trigones; plants usually relatively large; over 600 μm wide with leaves. Leaf lobes sharp (leaves all bilobed); many or all branches intercalary, lateral or dorsal; plants mostly ± brownish or infuscated to purplish, relatively rigid 9

9a. Shoot apices not running out into microphyllous, pigmented stolons; shoot tips never abruptly geotropic; branches *Frullania* type and/or lateral-intercalary, not displaced to dorsal end of leaf insertion. Gemmae sometimes present; leaves always bifid . . . . . *Anastrophyllum* (p. 673)

9b. Shoot tips of normal leafy stems running out into microphyllous, often geotropic (or strongly arched) flagelliform axes that are often pigmented; *Frullania*-type branches usually lacking, the branching in most taxa with intercalary branches from dorsal side of stem. Gemmae never present; leaves 2-lobed, rarely 0- or 3-lobed . . . . . *Andrewsianthus* (p. 685)

5b. Stems subhyaline, with (at least dorsally) a hyaloderm formed of few rows of large, hyaline cells surrounding a medulla of (usually) firmer-walled, mostly smaller cells; with stolons; leaf cells thin- or equally firm-walled, usually 18–38 μm wide; oil-bodies lacking. Underleaves absent, but gynoecia tristichous . . . . . *Metahygrobiella* (p. 553)

2b. Leaves remote, scale-like, bifid, closely appressed, often almost unresolvable; shoots filiform-julaceous, tiny 10

10a. Plants fuscous to black (perianths sometimes deeply vinaceous) . . . . . *Cephalomitrion* (p. 568)

10b. Plants whitish or locally vinaceous . . . . . *Cephaloziella* (p. 578)

1b. Leaves unlobed or, at most, retuse (rarely to 0.35 bilobed, sometimes crenulate and/or hyaline-margined; shoots very slender and julaceous) 11

11a. Shoot apices not abruptly geotropic and microphyllous; branches never from dorsal end of leaf axils. Leaves dorsally interlocking; plants slender, julaceous and ± suberect, with leaves unlobed or to 0.35 bilobed; perianth absent or short, usually included; gemmae lacking; underleaves lacking or vestigial; cells firm-walled 12

12a. Perianth distinct but included; innermost bracts usually largest 13

13a. Leaves crenulate with thin-walled, delicate cells, or smooth-margined; perianth pluriplicate, not compressed; dioecious . . . . . *Herzogobryum* (p. 788)

13b. Leaves irregularly denticulate with knob-like, thick-walled projecting marginal cells; perianth hardly plicate, narrowed and laterally compressed toward mouth; autoecious. . . . . *Nothogymnomitrion* (p. 795)

12b. Perianth none; innermost bracts variable, reduced, ± scale-like, hidden within larger outer bracts . . . . . *Gymnomitrion* (p. 805)

11b. Shoot apices abruptly geotropic and becoming microphyllous/leafless; branches from dorsal end of leaf insertions. Surface coarsely papillose . . . . . *Andrewsianthus* (p. p.) (p. 685)

Group J. Plants with leaves succubous, non-complicate, alternate and bilobed (margins edentate or dentate); rhizoids scattered, usually frequent (sometimes none on upper shoot sectors). Underleaves usually small or lacking. (Artificial group, including *Lophozioideae*, *Acrobolbaceae*, *Cephaloziellaceae*, *Cephaloziaceae*, etc.)

1a. Underleaves distinct, area usually at least 0.1–0.2 that of leaves in size. Plants mostly medium to large in size, over 0.8 mm wide 2
2a. Underleaves rectangulate, deeply bifid, lacking lateral cilia or teeth; perianth lacking, a subterranean, rhizoidous marsupium developed. Branches ventral-intercalary only; plants opaque, yellowish green . . . . . *Geocalyx* (vol. 2)
2b. Underleaves undivided and lanceolate, or 2- or 3-fid, if divided, with ± cilium formation; perianth distinct, without a marsupium 3
3a. Dorsal leaf margins not deflexed; leaf margins (except basally) edentate. Plants lacking stolons or flagella; perianth terete, plicate and contracted above. 4
4a. Leaf surface with coarse, often dense or contiguous papillae 5
5a. Trigones coarse, knot-like; stems paraphyllose; perianth plicate to base, not twisted; ♀ bracts not reduced . . . . . *Chandonanthus* (p. 640)
5b. Trigones not nodose; stems smooth; perianth plicate above only, the plicae twisted; ♀ bracts reduced in size, laciniate. Southern South America . . . . . [*Roivainenia*]
4b. Leaf surface with papillae low or none, the stem smooth. Trigones not knot-like; ♂ bracts neither laciniate nor reduced in size; rhizoids all dispersed; ventral-intercalary branches lacking; leaves 0.25 or more bilobed; often with gemmae . . . . . *Lophozia s. lat.* (p. 645)
3b. Dorsal leaf margins ± deflexed (a cnemis developed); leaf apices and/or margins usually toothed or shallowly bilobed. Androecia spicate, tapered 6
6a. Perianth laterally compressed, wide at mouth; leaf apices ± toothed; underleaves free, usually ciliiform or ciliate . . . . . *Plagiochila* (vol. 2)
6b. Perianth plicate, narrowed above; leaf apices to 0.2 bilobed, edentate; underleaves connate with leaves on one side, lanceolate. Southern South America . . . . . [*Nothostrepta* (p. p.)]
1b. Underleaves vestigial (subulate or lanceolate, few-celled; under 0.2 leaf length at most), or absent 7
7a. Branches, all or the large majority, lateral, intercalary and/or terminal (intercalary branches sometimes from ventral end of leaf axil) 8
8a. Perianth lacking, a pendulous marsupium developed; branching wholly intercalary; plants green to yellow-green, the stems whitish with age. Surface usually rough; oil-bodies large, often opaque 9
9a. Plants creeping, with rhizoids on leading leafy axes, stem under 14 cells in diam., without a distinct cortex, a system with a leafless/microphyllous caudex and stolons lacking; antheridia 1(2) per bract . . . . . *Acrobolbus* (vol. 2)
9b. Plants with ascending or erect leafy shoots from a leafless/microphyllous pale caudex, often with stolons or flagella, with rhizoids restricted to leafless axes below, the stem 16 cells or more high, with ± distinct cortex; antheridia 2–15 per bract 10
10a. Gametangial branches usually abbreviated, then often whitish, from lower ends of leafy shoots; ♀ bracts often mere inconspicuous scales; antheridia 2–4(5) . . . . . *Marsupidium* (p. p.) (vol. 2)
10b. Gametangia on leading, leafy, erect stems; ♀ bracts large, leaf-like, the innermost ones distinct; antheridia 5–15 . . . . . *Tylimanthus* (p. p.) (vol. 2)

8b. Perianth present, a marsupium lacking; branching variable; plants not opaque green above and whitish on older sectors 11
11a. Perianth wide at the laterally compressed mouth; leaves often with a cnemis, the dorsal margin abruptly decurved; leaf margins and/or lobes usually sparingly to copiously dentate, the teeth usually sharp, spinose. Leafy shoots from a rhizoidous basal caudex 12
12a. Leaf surface mostly smooth, at most finely papillose, the papillae low . . . . . *Plagiochila* (vol. 2)
12b. Leaf surface coarsely papillose, the papillae dense, hemispherical, distinctly protruding . . . . . *Dinckleria* (vol. 2)
11b. Perianth not laterally compressed; leaves never with a cnemis; leaf margins usually edentate. Perianth plicate, moderately contracted to mouth; seta of the general type: at least 6–8 cells in diam. . . . . *Lophozia* (p. 645)
7b. Branches, all or predominantly, ventral-intercalary. Stolons or flagella present in many taxa 13
13a. Leaves with ventral margins not conspicuously decurved; seta reduced, of 4 or 8 outer + 4 inner cell rows 14
14a. Dorsal end of leaf insertion essentially transverse, extended to stem midline dorsally; gemmae usually lacking; perianths on leading axes . . . . . *Metahygrobiella* (p. 553)
14b. Dorsal end of leaf insertion oblique, not extended to stem midline dorsally; gemmae often present; perianths usually on abbreviated branches . . . . . *Cephalozia* (p. 559)
13b. Leaves with ventral margin strongly deflexed, leaf apices shortly bifid; seta ca. 10 cells in diam. Southern South America . . . . . .[*Nothostrepta* (p. p.)]

Group K. Leaves with insertion (and usually orientation) perceptibly succubous, the adaxial lamina usually ± turned toward the observer; leaves alternate, unlobed, edentate or variously dentate/ciliate; rhizoids always scattered. Branches normally all intercalary. Most taxa with vestigial or no underleaves.

1a. Cells on abaxial surface of leaf with large dome-like to mammilliform thickenings; gametangia on abbreviated lateral-intercalary branches or on leading shoots. Perianth present 2
2a. Surface of leaf with large dome-like to mammilliform thickenings each positioned over the cell lumen, the dome-like thickenings with dense hemispherical to clavate papillae; gametangia on abbreviated lateral-intercalary branches; plants prostrate and loosely creeping, typically corticolous (very rarely saxicolous) . . . . . *Brevianthus* (vol. 2)
2b. Surface of leaf with large dome-like thickenings each positioned over the radial walls (not over the cell lumen), the dome-like thickenings smooth; gametangia on leading shoots; plants erect, in cliff crevices or over soil . . . . . *Bragginsella* (vol. 2)
1b. Cells smooth or, if papillose, without dome-like thickenings associated with each cell; gametangia on abbreviated ventral-intercalary branches. Plants suberect to erect 3
3a. ♂ and ♀ Branches reduced in size, abbreviated, normally all ventral-intercalary (usu-

ally produced only from older, lower sectors of, often, small-leaved or microphyllous axes). Leaf cell trigones lacking to large, rarely nodose 4

4a. Perianths lacking; a pendent marsupium developed, or an erect, fleshy perigynium on weak ventral-intercalary branches. Androecia small, spicate, ± determinate; vegetative branches all or mostly ventral-intercalary 5

5a. Plants green to fuscous, but not pitch black, the leafy shoots erect; with leafy shoots arising from an extensive system of plagiotropic and geotropic leafless axes; trigones ± concave-sided 6

6a. Gynoecium producing an erect, fleshy, ± clavate calyptral perigynium, invested beneath by an isomorphic ring of bracts + bracteole 7

7a. Stem to 25 cells in diam,, with a 2–3-layered firm-walled cortex; plants small, usually olive-green to brownish; gemmae often present. Capsule wall 4–6-stratose . . . . . *Adelanthus* sect. *Calyptrocolea* (p. 616)

7b. Stem to 35–40 cells in diam., with a collapsing hyaloderm surrounding thick-walled cells within; plants vigorous, pure green; gemmae lacking. Capsule wall 6–7-stratose; leaves copiously toothed . . . . . *Wettsteinia* (p. 628)

6b. Gynoecia producing a pendent marsupia, at summit with vestigial bractlets. Plants green, older sectors (more or less) ivory white . . . . . *Marsupidium* (vol. 2)

5b. Plants brown or black, creeping and forming compact mats, the shoots all leafy, without a small-leaved caudex (but geotropic stolons often present); trigones nodose. Gynoecia producing marsupia . . . . . *Jackiella* (p. 634)

4b. Perianths developed, usually conspicuous, trigonous. Plants erect, the leafy shoots smaller-leaved below, arising from a creeping, microphyllous, rhizoidous caudex; underleaves lacking or vestigial; leaves unlobed, bidentate or pluridentate; seta massive, over 6 cells in diam. 8

8a. Leaf apices entire or variously toothed, never bidentate; stems usually fuscous pigmented, darker than the leaves, the cortex 2–3-layered, the cortical cells very thick-walled and with greatly reduced lumina; plants often developing gemmae . . . . . *Adelanthus* (p. p.) (p. 615)

8b. Leaf apices (in ours) with 2 strong spiniferous teeth; stems unpigmented (except *P. aureocinctum*), usually not darker than leaves, the cortex in 1(2) layers, the cortical cells at most moderately thick-walled; plants lacking gemmae . . . . . *Pseudomarsupidium* (p. 609)

3b. ♀ + ♂ Gametangia not on reduced branches, the ♀ terminal on long leafy shoots, the ♂ becoming intercalary on leafy shoots. Branches often of lateral-intercalary and *Frullania* types, usually not exclusively ventral-intercalary 9

9a. Leaves narrow, elongated, acutely pointed, edentate, the summit long-protracted. Perianth terete, plicate; leaves spreading, in drying dorsally ± secund; ♂ bracts with lobule long-acuminate distally . . . . . *Cuspidatula* (p. 726)

9b. Leaves various in shape, never ovate or ovate-lanceolate and pointed 10

10a. Perianth distinct, well developed (only rarely hidden between bracts at maturity) 11

11a. Perianth distally sharply laterally compressed, wide and bilabiate at mouth 12

12a. Leaves inserted dorsally to the stem midline, or beyond, a leaf-free dorsal strip lacking; cortex well defined, medulla mycorrhiza-free; caudex and/or stolons freely formed; leaves mostly dentate/ciliate; dioecious . . . . . *Plagiochila* (vol. 2)

12b. Leaf insertion not attaining stem midline dorsally; cortex scarcely distinct, medulla mycorrhizal; caudex and stolons lacking; leaves unlobed or retuse, edentate; autoecious . . . . . *Pedinophyllum* (vol. 2)

11b. Perianth terete, at least in basal 0.5–0.7, never bilabiate, ± constricted above 13

13a. Branches all, or predominantly, terminal-lateral, or axillary (in middle or ventral halves of leaves; gynoecia with bracts unlobed, edentate, without accompanying bracteole; plagiotropic caudex lacking, but some taxa with stolons. Basal perigynium usually at least weakly developed (strongly developed in some taxa); perianth with beak present or absent, if present, then the rostellum never depressed and situated at the truncate summit of the perianth; perianth mouth crenulate or entire; plants nearly always developing reddish or vinaceous pigments; leaves various, mostly orbicular or ovate; underleaves wholly absent, even in gynoecial regions . . . . . *Solenostoma* (p. 694)

13b. Branches all, or predominantly, intercalary, from ventral end of leaf axils or ventral (in some taxa some terminal-lateral, *Frullania*-type branches developed); gynoecia with bracts + bracteole usually variously lobed and/or incised, often reduced in size; plagiotropic microphyllous axes and stolons usually frequent (except in *Jamesoniella*) 14

14a. Leafy shoots bearing or arising from a caudex and/or stolons; terminal branches usually absent. Trigones not coarsely nodose, not bulging and prismatic; perianth mouth crenulate or entire; plants nitid, deep brown to red-brown . . . . . *Cryptochila* (p. 732)

14b. Leafy shoots not arising from a caudex; stolons lacking; terminal, *Frullania*-type branches present . . . . . *Jamesoniella* (p. 713)

10b. Perianth lacking, with a marsupium or marsupium precursor. Underleaves lacking; rhizoids all scattered; perianth absent; branches (all or most) lateral 15

15a. Leaves clearly alternate 16

16a. Plants creeping to prostrate, rhizoidous all along leafy axes, a caudex lacking 17

17a. Stem 15 or more cells in diam.; ♂ bracts with 3–9 or more antheridia; marsupia slenderly cylindrical, subterranean . . . 18

18a. Leaves edentate; plants ± flat, green to warm brown; gemmae often present . . . . . *Lethocolea* (vol. 2)

18b. Leaves (more or less) toothed, rarely entire; plants julaceous, the leaves strongly concave, ± purplish pigmented; gemmae absent . . . . . *Goebelobryum* (vol. 2)

17b. Stem slight: ca. 8 cells in diam.; ♂ bracts 1-androus; marsupia conoidal, not penetrating substrate. Leaves round, edentate, concave . . . . . *Acrobolbus* subg. *Lethocoleopsis* (vol. 2)

16b. Leafy shoots erect or stiffly ascending, lacking rhizoids except on small-leaved bases and caudex . . . . . *Tylimanthus* (vol. 2)

15b. Leaves opposite . . . . . see Couplet 12, Group H

Group L. Plants with leaves complicate-bilobed (often abaxially winged) and/or with elaboration of a ventral, specialized water sac. Underleaves lacking.

1a. Rhizoids either scattered on stem or in bundles at ventral bases of leaves; infra-axillary branches lacking 2

2a. Rhizoids in defined fascicles, from ventral bases of normal leaves. Branches of *Frullania* and ventral-intercalary types 3

3a. Keel elongated, 0.35–0.5 leaf length, the leaf spatulate, U-shaped in section; cells with trigones coarse (often confluent) in distal parts of leaf, at base narrowly rectangulate, forming a vitta; gemmae and underleaves lacking . . . . . *Blepharidophyllum* (p. 779)

3b. Keel short, 0.15–0.35 leaf length, sharply folded and complicate, not spatulate; cells thin- to equally firm-walled, the leaf lacking a distinct vitta; gemmae on erect, microphyllous shoots with underleaves . . . . . *Clandarium* (p. 774)

2b. Rhizoids scattered, never in bundles, sometimes few or none 4

4a. Perianth lacking, a coelocaule present; dorsal lobe ± larger than ventral (if not, a wide wing separating the two); rhizoid apices often digitately branched; asexual reproduction absent 5

5a. Dorsal lobe flat, slightly larger than ventral, broadly margined with vitreous, hyaline cells; monandrous. New Caledonia . . . . . [*Perssoniella*]

5b. Dorsal lobe usually convex, not larger than ventral, not margined with hyaline cells; polyandrous . . . . . *Paraschistochila* (vol. 2)

4b. Perianth distinct, plicate and/or flattened dorsiventrally; dorsal lobe 0.25–0.7(0.85) area of ventral lobe; rhizoid apices never digitate; asexual reproduction via catenulate gemmae 6

6a. Leaves with keel U-shaped, the leaves basally spatulate, the keel at most sharp near its apex; gemmae polygonal or stellate, or lacking; perianth plicate, moderately compressed 7

7a. Leaf lobes unequal: the dorsal at most 0.75 the ventral in size; leaf lobes non-squarrose, or dorsal squarrose; plants green to brown, sometimes with red pigments, never piceous. Gemmae present, stellate or polygonal . . . . *Diplophyllum* subg. *Diplophyllum* (p. 747)

7b. Leaf lobes subequal, both strongly squarrose; plants often dark brown to fuscous, opaque . . . . . *Diplophyllum* subg. *Austrodiplophyllum* (p. 747)

6b. Leaves sharply folded in keelar region, the bases not sheathing, the keel usually ridged or winged (at least distally); gemmae usually ellipsoidal, smooth; perianth usually strongly compressed, smooth . . . . . *Scapania* (p. 767)

1b. Rhizoids either in bundles from the ventral lobe (lobule) of the leaf or occurring in small groups (2–few) at intervals on the stem; branches all infra-axillary, arising posterior to a leaf. (Taxa with strongly complicate-bilobed leaves, with ventral lobe smaller, folded under the larger, incubous, dorsal lobe. Usually yellow-green or green; often with asexual reproduction.) 8

8a. Rhizoids lacking from stem, arising as small fascicles from the ventral leaf lobes (lobules); perianth strongly dorsiventrally flattened, wide and truncate at mouth . . . . . *Radula* (vol. 3)

8b. Rhizoids occurring isolated, or in bundles of 2–few, at regular intervals on stem (at points where underleaf formation has been suppressed); perianth 5-angled or ± compressed, but always contracted abruptly into a small beak 9

9a. Branches all with a low basal collar; gemmae usually intramarginal; leaves never sharply dimorphic . . . . . *Cololejeunea* (vol. 3)

9b. Branches athecal, smoothly joined to stem; gemmae usually marginal; leaves dimorphic: some lobulate, others elobulate . . . . . *Aphanolejeunea* (vol. 3)

Group M. Plants strongly complanate, with leaves complicate-bilobed, with 1 (2 in *Goebeliella*) smaller, inflexed ventral lobe(s), hidden in dorsal aspect of plant, the lobules ± transformed into a water sac (except *Porella*). Underleaves large, conspicuous, unlobed; branching only lateral; rhizoids only at underleaf bases. Perianths (but no other perigynoecial structures) developed. (*Lejeuneaceae* subfam. *Ptychanthoideae* + *Porellaceae* + *Goebeliellaceae*.)

1a. In ventral aspect, a single lobule visible; leaf cells in distal part of lamina lacking hyaline, perforated cells 2

2a. Lobule oriented nearly parallel to stem, not converted to a water sac, lying at nearly right angles to lobe, with margins reflexed and organs all on short lateral branches . . . . . *Porella* (vol. 3)

2b. Lobule with longer axis oriented parallel to lobe, united to it by a long keel, inflated at least along keel, with free margins never reflexed and organs (in ours) always on elongated branches or at apices of main stems. (*Lejeuneaceae* subfam. *Ptychanthoideae*) 3

3a. Perianths never sharply 5-carinate: with 3 plicae or keels, or with 4 winged or armed keels, or up to 8–10 plicate. Usually deep brown to blackish 4

4a. Stem with cortex of thick-walled cells in many rows (underleaves attached to stem by many cells). Cells with 2–8(10) large, botryoidal, opaque oil-bodies. Leaves and underleaves often dentate. Subfloral innovations present 5

5a. Branching regularly, thecal (*Lejeunea* type); perianth 3-carinate . . . . . *Mastigolejeunea* (vol. 3)

5b. Branching all or mostly athecal (*Frullania* type); perianth pluriplicate . . . . . *Ptychanthus* (vol. 3)

4b. Stem with cortex of thin- or slightly thick-walled cells (diam. superior to that of medullary cells), in few, usually 12–16 rows (underleaves attached by usually 2–4 ventral cortical cells). Oil-bodies numerous, very small, homogeneous and glistening, or few partite with age. Leaves and underleaves edentate. No subfloral innovations 6

6a. Plants golden to inky black, glossy, nearly flat when dry and when moist; gynoecia with toothed bracts; perianth flattened, with 4 winged (and sometimes armed and/or lamellate) keels; underleaves orbicular to reniform; trigones, if distinct, never cordate. (Dioecious or autoecious.) . . . . . *Lopholejeunea* (vol. 3)

6b. Plants golden brown or fuscous to brown-black, never inky, not nitid, when dry with leaves convolute, when moist spreading; gynoecia with neither bracts nor perianth keels toothed or lamellate; perianth with ca. 8–10 rounded plicae, the plicae smooth, rounded; underleaves obdeltoid; trigones conspicuous, cordate. (Our taxa paroecious.) . . . . . *Acrolejeunea* (vol. 3)

3b. Perianths sharply 5-carinate (dorsal keel sometimes low and short), the carinae smooth. Plants dull, deep green to brown; with 1–2 innovations; oil-bodies many (in ours to 20–40 per cell), small, few-segmented; stem lacking a distinct hyaloderm of enlarged cells. (Our spp. dioecious.)
. . . . . *Archilejeunea* (vol. 3)

1b. In ventral aspect, each leaf is provided with 2, curved, horn-like, inflated lobules; leaf cells, distally, dimorphic: some hyaline and perforate; at base leaves with linear cells (*Goebeliellaceae*) . . . . . *Goebeliella* (vol. 3)

Group N. Similar to Group M (leaves basically complicate-lobed, often with a smaller, inflexed ventral lobe = lobule); branching only lateral (in *Balantiopsaceae* sometimes also ventral-intercalary). Differing in the 2- or 4-lobed underleaves. (*Balantiopsaceae*, *Schistochilaceae* p. p., see Group L for *Paraschistochila*.)

1a. Leaf cells strongly elongated, rectangulate, often tiered; branches never infra-axillary, in part ventral-intercalary; marsupium developed . . . . . *Balantiopsis* (vol. 2)

1b. Leaf cells neither strongly elongated nor tiered; branches often infra-axillary (and never ventral-intercalary); marsupium absent, a coelocaule developed 2

2a. Rhizoids scattered, claret-red, their apices often dendritically, ramified but not digitate, their branches often coalescent, not or sparingly septate; leaves 1-stratose, often pigmented, often ± toothed or ciliate . . . . . *Schistochila* (vol. 2)

2b. Rhizoids in fascicles from underleaf and ventral leaf bases, colorless, apices often divided into multiseptate, finger-like digits; leaves normally polystratose, at least locally, clear green, mostly edentate or with few, broad-based teeth
. . . . . *Pachyschistochila* (vol. 2)

Group O. Complanate plants, with complicate-bilobed lateral leaves; lobules of stem leaves (and/or branch leaves) galeate or helmet-shaped, longer than wide, only feebly attached to (and often remote from) stem; water sac formed only by the inflated sac-like lobule; underleaves distinct, 2- or 4-lobed. (*Lepidolaenaceae*, *Jubulopsaceae*, *Frullaniaceae*.)

1a. Leaf lobes (and usually underleaves) variously ciliate or toothed; underleaves 2- or 4-

lobed; perianth reduced or lacking, a clavate, paraphyllose or lamella-bearing coelocaule produced 2

2a. Underleaves of stems and branches all 2-lobed, with reflexed margins, no underleaf lobes converted into water sacs. Coelocaule hidden by imbricate, mutually involute bracts + bracteoles . . . . . *Gackstroemia* (vol. 2)

2b. Underleaves of main stems, at least, all deeply 4-lobed. Coelocaule not wholly obscured by bracts + bracteoles 3

3a. Branch underleaves never with lobes converted to water sacs, 2- or 4-lobed. Coelocaule club-shaped, covered with multiform lamellae . . . . . *Jubulopsis* (vol. 2)

3b. Branch underleaves deeply 4-lobed, two of which are converted into water sacs 4

4a. Plants soft-textured, pale green, spongy, never reddish. Main stems paraphyllose. Coelocaule slenderly clavate. (On peaty ground or soil.) . . . . . *Lepidogyna* (vol. 2)

4b. Plants firm, deep green, but usually reddish to red-brown pigmented, much like *Frullania*. Stems smooth. Coelocaule obpyriform to short-clavate. (Usually epiphytic.) . . . . . *Lepidolaena* (vol. 2)

1b. Leaves with lobe margins entire (except *Frullania chevalieri*, which has lobe margins crenulate denticulate); underleaves 2-lobed, lobes edentate. Perianth conspicuous, without a coelocaule at base . . . . . *Frullania* (vol. 3)

Group P. Plants with stem leaves developing distinct, galeate lobules (water sacs) formed by the infolded ventral lobe and the opposed basal portion of the lobe, the lobules attached by an elongate keel to the lobe. Plants pale to yellowish to grass-green. Vegetative branches thecal, with a distinct basal sheath (except at times in *Nephelolejeunea*). (*Lejeuneaceae.*)

1a. Underleaves normal in number: one per pair of lateral leaves (segmentation helical); underleaves usually not with divergent slender lobes 2

2a. Leaves constricted basally, with abbreviated, subtransverse insertion on stem: lobule attached by only 1–2(3) cells to stem; lobes narrow, usually obovate, elongated; underleaves remote, small, narrow, with very narrow lobes; sometimes with discoid pluricellular gemmae from surface cells. (*Tuyamaelloideae*) 3

3a. Lobule with 1(2) distinct to indistinct apical teeth 4

4a. Lobule linear, the apical tooth formed of 2 rounded, projecting cells, with hyaline papilla inserted between the teeth, thus externally visible; lobe spatulate-obovate, rounded distally . . . . . *Siphonolejeunea* (vol. 3)

4b. Lobule obovoid-cuneate, the apical tooth single, formed of 2 superposed cells, the hyaline papilla entally displaced to base of tooth; lobe rounded or sharply pointed . . . . . *Nephelolejeunea* (vol. 3)

3b. Lobule with 3 distinct teeth distally, the median largest. Lobule obovoid-cuneate, with hyaline papilla entally displaced; lobes narrowly obovate, rounded distally . . . . . *Austrolejeunea* (vol. 3)

2b. Leaves with a J-shaped insertion line: the insertion not constricted, the lobe insertion running up stem (longer arm of J); lobule broadly attached to stem by 5–6 or more cells (short arm of J); never with discoid gemmae (in New Zealand) 5

5a. Leaf margins neither lobulate nor toothed; lamina smooth, unarmed; underleaf bilobed but lobes and disc unarmed on margins; mostly not epiphyllous 6

6a. Underleaves subrotundate to ovate or obovate, with erect lobes (which are always over 2 cells wide at base on stem underleaves); leaves without ocelli (except in *Rectolejeunea*, which has caducous leaves); lobes usually rounded (except *Stenolejeunea*), not elongated: length:width ca. 1.1–1.2:1 7

7a. Lobules of stem leaves with hyaline papilla inserted in a faint notch just proximad of the 1-celled apical tooth; plants usually clear to yellowish to whitish green, mostly rather translucent; cells with (1–3)4–many small, glistening or granular oil-bodies. 8

8a. Leaf lobes rounded, never with sharp tips ending in 2 superposed cells; no asexual reproduction (or, *Rectolejeunea*, with caducous leaves); surface (in ours) smooth 9

9a. Leaves persistent, lacking ocelli; perianth 5-keeled or inflated, never compressed; marginal cells over 12 μm . . . . . *Lejeunea* (vol. 3)

9b. Leaves caducous, the lobes ocellate; perianth compressed, the dorsal keel vestigial or weak; marginal cells only ca. 8 μm . . . . . *Rectolejeunea* (vol. 3)

8b. Leaf lobes, especially on branch leaves, apiculate, sharp, ending often in 2 superposed cells; with thalloid, elongating propagulae from lobe margins (which also develop marginal rhizoids); surface minutely granular . . . . . *Stenolejeunea* (vol. 3)

7b. Lobules (always well developed) with hyaline papilla in sinus, distad of the apical tooth; plants rather firm: walls thick, or trigones conspicuous, often rather opaque and whitish green or grey-green; cells with 1–2(4) very large, coarsely botryoidal oil-bodies . . . . . *Cheilolejeunea* (vol. 3)

6b. Underleaves narrow-based, obdeltoid, with strongly divergent lobes; leaves with ocelli of lobe base (and often also laminar ocelli); lobes elongated, elliptical to falcate (then acute to acuminate), length:width ca. 2–4:1. Caducous leaves lacking: asexual reproduction, if present, via short caducous branches from leading axes (= cladia). (Small or tiny, rather pellucid, light green, delicate plants.) 10

10a. Ocelli (in ours) basal, (0)1–2 per lobe; leaf lobes sharp to acuminate; gynoecia always with 1–2 innovations; median cells (in ours) with 1 or 2–4 granular oil-bodies; underleaves without a conspicuously small-celled basal field, the marginal cells not differentiated; plants never intensely fragrant when alive 11

11a. Median cells (in ours) with 2–4 oil-bodies; leaf lobes decurved, cuspidate; underleaf lobes blunt to rounded, ca. 4 cells wide at base; gynoecia (in ours) on long to short shoots, with 1–2 *Lejeunea*-type innovations (first appendage of innovation a lateral leaf) . . . . . *Harpalejeunea* (vol. 3)

11b. Median cells (in ours) with 1 oil-body; leaf lobes attenuate, subacuminate, erect to suberect; underleaf lobes few-

celled, long-acute; gynoecia (in ours) on short branches, with 1 innovation of *Pycnolejeunea* type (first appendage an underleaf) . . . . . *Drepanolejeunea* (vol. 3)

10b. Ocelli 6–8(9) per lobe, in a broken (interrupted) median line + a few ocelli distally scattered; leaf lobes elliptical-lingulate, blunt to rounded, in drying standing stiffly away from substrate; gynoecia lack innovations, on very short branches; median cells with 7–11 oil-bodies; underleaves transversely rectangular, margined by 6 very large cells contrasted to a small-celled field within; lobes uniseriate, widely separated, few-celled; plants intensely fragrant when alive . . . . . *Leptolejeunea* (vol. 3)

5b. Leaf margins variously lobulate-dentate or dentate (at least above); lamina smooth or hispid; underleaves with margins crenulate or dentate; always epiphyllous, on mosses, ferns, and seed plants. Lobules inflated, strikingly so, the entire free (anterior) margin conspicuously involute, the apical tooth never apparent without dissection 12

12a. Lobes appearing lobulate-crispate, due to reflexed, lunate marginal sectors, and lobes distally denticulate; lobe and perianth surfaces smooth; underleaves with entire lobe margins, lobes divergent and rounded, margins crenulate . . . . . *Kymatolejeunea* (vol. 3)

12b. Lobes not crispate and lobulate, merely gently convex, with both margins and surfaces spinose-armed; perianth surface also spinulose; underleaves with margins spinulose, the lobes sharp and erect . . . . . *Echinolejeunea* (vol. 3)

1b. Underleaves duplicated: one for each lateral leaf (segmentation pendular); underleaves with very slender, usually divergent, lanceolate to linear-lanceolate lobes. Leaf insertion on a short base, the leaves constricted at base. (Sometimes with discoid gemmae.). 13

13a. Leaves obovate or rotundate-obovate, with lobule smaller than and clearly distinct from lobe; oil-bodies granular . . . . . *Diplasiolejeunea* (vol. 3)

13b. Leaves complex: the enlarged (hardly recognizable) lobule forming a water sac, opening by a flap, formed jointly with the reduced dorsal lobe: the lobule apex produced as a tumid or horn-like, inflated sac; oil-bodies homogeneous . . . . . *Colura* (vol. 3)

Suborder 1. **LEPICOLEINEAE** R.M.Schust.

Jungermanniales suborder *Lepicoleineae* R.M.Schust., J. Hattori Bot. Lab. 36: 336. 1972.

The *Lepicoleineae*, for the most part southern temperate in distribution, is comprised of two families, each with a single genus. In addition to the regional *Lepicoleaceae* the suborder includes *Vetaformaceae* Fulford & J.Taylor, a monotypic family with only *Vetaforma dusenii* (Steph.) Fulford & J.Taylor of southern South America; for details see Fulford (1963b), Hässel and Solari (1976) and Schuster (2000a).

Family **LEPICOLEACEAE** R.M.Schust.

Lepicoleaceae R.M.Schust., Nova Hedwigia 5: 27. 31 Jan. 1963. R.M.Schust. *ex* Fulford, Mem. New York Bot. Gard. 11: 30. 15 March 1963. R.M.Schust., Rev. Bryol. Lichénol. 26: 126. 1957, *nom. inval.*

Plants isophyllous or nearly so, stiff, erect or suberect, at times pendent, pale green to greyish green to golden brown; shoots large, to 10–15 cm long. Branching rather regularly 1-pinnate, the branches predominantly of *Frullania* type, typically determinate in length, drooping and curved toward shoot base, tapering, becoming microphyllous and flagelliform, at times long and whip-like, often cernuous; lateral-intercalary branches less frequent. Stems rigid, smooth in ours but paraphyllose in some nonregional species, in cross section with cortex in (1)2–3 or more layers of very thick-walled cells grading into the larger, thick-walled medullary cells. Rhizoids colorless, sparing, at bases of microphyllous underleaves and leaves of flagelliform sectors of branches, rarely at bases of underleaves on main shoot. Leaves with insertion weakly incubous, symmetric to slightly asymmetric, bisbifid, the median sinus descending to 0.45–0.75 or a little more; lobes typically narrow and long-attenuate, frequently with hyaline and/or setaceous tips; lamina (and sometimes lobe) margins often dentate to ciliate-laciniate. Cells with thick walls and massive, ± confluent trigones; cells in median sector of lamina (and, less conspicuously, those in basal half of lobes) sometimes ± elongate and forming a weakly to distinctly defined vitta; surface striate-papillose or striolate. Oil-bodies (*fide* Schuster, 2000a) homogeneous, 2–5 up to 5–10 per cell. Asexual reproduction lacking. Underleaves transversely inserted, with shape, size and form much like the leaves. Asexual reproduction by fragmenting lobe apices in some taxa, exceptionally via regeneration.

Plants dioecious (in our species) or rarely monoecious. Androecia becoming intercalary on leading shoots, only weakly differentiated from vegetative sectors. ♂ Bracts usually bisbifid, ventricose at base; bracteoles sometimes with antheridia, the bracteoles then similar in form to bracts; antheridia 1–2 per bract (and bracteole), the stalk short, biseriate. Gynoecia terminal on main shoot or on rather short to long branches, with bracts and bracteoles basically similar to leaves and underleaves, the innermost becoming fragmented as scales on the coelocaule. Sporophyte protected by an erect, clavate, thick-walled coelocaule, the surface with variably modified bracts, bracteoles and sometimes also paraphyllia lending a bristly and "head-like" appearance; free calyptra absent.

Seta massive, short, barely elevating the capsule beyond the coelocaule. Capsule spherical, ca. 1 mm in diam., opening by 4 slits, the wall 5–7-layered, the outer layer of cells with two-phase ontogeny, the well-developed nodules restricted to the irregularly oriented secondary walls; innermost layer of cells with nodular thickenings, the thickenings tending to coalesce and form weak, irregular, continuous sheets of material, with semiannular bands rare or lacking.

Spores aculeate to tuberculate, ca. 2–4× elater diam. Elaters rather short, tortuous, bispiral.

Type: *Lepicolea* Dumort.

The genus has about 10 species and is widely distributed within south-temperate–circum-Pacific areas. *Lepicolea ochroleuca* (Spreng.) Spruce is an amphi-Atlantic species, occurring in South Africa, Tristan da Cunha, Falkland Islands, southern South America, Juan Fernandez Islands, northern Andes; also in Central America and Mexico. Two species occur in southern South America in addition to *L. ochroleuca*; these are *L. rigida* (De Not.) E.B.Scott and *L. magellanica* (Gola) Solari. Two species are found in New Zealand.

Lepicolea Dumort.

Lepicolea Dumort., Recueil Observ. Jungerm. 20. 1835.

Type: *Lepicolea scolopendra* (Hook.) Dumort. *ex* Trevis. (≡ *Jungermannia scolopendra* Hook.)

Lepicolea species typically occur on trunks and more often branches of trees, and sometimes form colonies or extensive masses that, in some cases, become pendulous. The species are often abundant in exposed niches (such as at the edge or canopy of the forest or on rock walls), where illumination is good, if intermittent, and where the sun regularly alternates with atmospheric moisture, such as fog or mist. *Lepicolea* species are apparently efficient colonizers, and may be locally abundant in some areas, with many trees that bear scattered populations of various sizes. The species are much less frequent in shaded, protected niches, e.g., they are sparse deep within the forest.

References: Scott (1960; revision); Stewart (1978; oil-body data of regional species); Schuster (2000a).

Key to Species

1a. Plants bristle-like, the distal sector of leaf lobes hyaline and setaceous; leaf lobes with uniseriate row (420)490–630 μm long, the terminal cell length:width ratio 6–13:1, the second and third cells from tip (2.8)3–11:1, the fourth cell 2–4:1; surface of uniseriate row of leaf lobes finely striate; vitta well developed . . . . . *L. scolopendra* (p. 99)

1b. Plants not bristle-like, the distal sector of leaf lobes green and acuminate; leaf lobes with uniseriate row 130–215 μm long, the terminal cell length:width ratio 1–5:1, the second and third cells from tip at most 3:1, the fourth cell (when present) normally subquadrate; surface of uniseriate row of leaf lobes papillose; vitta indistinct . . . . . *L. attenuata* (p. 95)

Lepicolea attenuata (Mitt.) Steph.

[Plate 1D; Figs. 6, 7: 1–6]

Sendtnera attenuata Mitt. *in* Hooker, Bot. Antarc. Voy. 2: 153. *pl. 102, f. 2.* 1854. *Herbertia attenuata* (Mitt.) Kuntze, Rev. Gen. Plant. 2: 836. 1891. *Lepicolea attenuata* (Mitt.) Steph., J. Linn. Soc., Bot. 29: 276. 1892. Type: New Zealand, North Is., Bay of Islands, *Hooker* (NY!).

Sendtnera quadrifida Colenso, Trans. & Proc. New Zealand Inst. 21: 69. 1889 (1888). Type: New Zealand, Wairoa Co., high hills at Lake Waikare, 1888, *Hill* (Colenso a. 1422) (BM![=2]).

Plants stiff and wiry, pale green to golden brown; (20)60–70 mm long, 13–20(40) mm wide; shoots to 1.6 mm wide. Stems lacking paraphyllia. Leaves rigid, obliquely spreading, imbricate, subsymmetrically rectangular to narrowly long-ovate, the lamina often somewhat dilated dorsally; leaves 0.65–0.80 mm wide at level of median sinus, (1.1)1.3–1.6 mm long, quadrifid, the median sinus descending to 0.45–0.7, the marginal pair of sinuses often differing from one another in depth, the lobes acuminate to subcaudate, green throughout, the leaf lobes with uniseriate row 130–215 μm long, the terminal cell 1–5:1, 40–70 mm long, the second and third cells from tip at most 3:1, the fourth cell (when present) normally subquadrate,

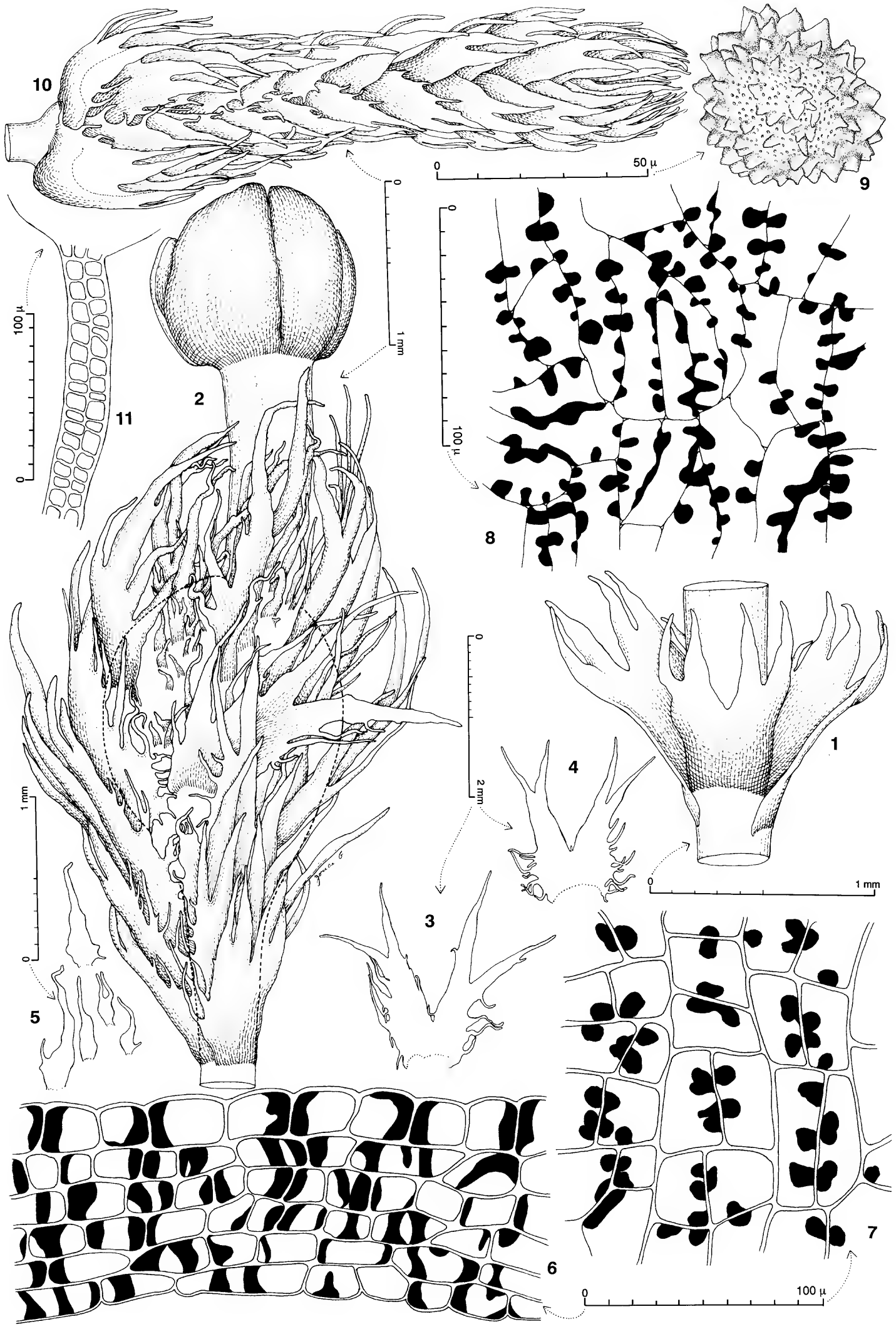

Fig. 6.
Lepicolea attenuata (Mitt.) Steph. 1. Sector of main shoot, ventral view. 2. Coelocaule with mature sporophyte, dorsal view. 3. Innermost ♀ bract. 4. Innermost ♀ bracteole. 5. Paraphyses from coelocaule. 6. Capsule wall, cross section. 7. Capsule wall, outer layer. 8. Capsule wall, inner layer. 9.

the segment margins entire; dorsal and ventral margins of lamina broadly curved, subauriculate at base, the marginal cells with swollen, protuberant septa giving a crenulate appearance, the dorsal margin otherwise coarsely ciliate-laciniate, the ventral entire, sporadically with a cilium. Vitta of leaves distinct, in median sector of lamina and extending to level of median sinus, or, less conspicuously, to middle of lobes, but not to the apices; cells of vitta elongate, near the leaf base 20–24 μm wide, 43–55 μm long. Leaf cells with massive trigones, the cells between vitta and margin in median sector of lamina 16–22 μm wide and long; surface of lamina coarsely striate-papillose, of uniseriate row of lobes papillose, of leaf base markedly long-striate. Oil-bodies 3–7 per cell, smooth, colorless, 4 × 4–6 μm, only visible in young leaves, not persisting. Underleaves ± clasping the stem, spreading, often widely so, imbricate, symmetric, the shape as in leaves, quadrifid, the median sinus descending to 0.6–0.8; lobes as in leaves; lamina margins crenulate as in leaves, otherwise entire or repand, sporadically with a cilium. Asexual reproduction by regeneration or by fragmentation of leaves from older parts of stems. Fungal partner absent.

Plants dioecious. Androecia restricted to branches, wider than sterile sectors of branch, terminal but eventually becoming intercalary; bracts in 3–8 pairs, less deeply lobed than leaves, the lamina ventricose; antheridia 1–2 per bract, the stalk and jacket-cells thick-walled. Gynoecia on branches with several, but never numerous, vegetative leaves; bracts of innermost series much larger than branch leaves, subobtrapezoid, quadrifid, the median sinus descending to 0.7–0.8, the lateral pair of sinuses much shallower, the lobes caudate, sulcate at least in basal half, the segment margins sparingly ciliate or entire; lamina margins rather copiously ciliate-laciniate-lobulate; bracteoles of innermost series as in bracts.

Seta to 2.3 mm long, 10–11 cells in diam., with 48 rows of epidermal cells surrounding an inner core of scattered cells similar in size to epidermal cells. Capsule wall 96–106 μm thick, of 6 layers; outer layer of cells subquadrate to short-rectangular, with two-phase type of distribution of thickenings, the radial walls with broad-based nodules that tend to cluster on opposing sides of a radial wall; innermost layer of cells highly irregular in shape, the radial walls with dense nodular thickenings that are sometimes confluent at the base, the walls with semi-annular bands sporadic.

Spores 40–44 μm in diam. (including conical projections), brown, aculeate, the surface with fine papillae between the conical projections. Elaters tortuous, 10.6–11 μm wide, bispiral, strongly tapered toward the tips, the tips slender, each with a nonspiral thickening.

Distribution and Ecology: Endemic to New Zealand: South Island (120–1130 m) and North Island (300–1220 m). Known from Fiordland, Westland, Canterbury, Western Nelson, Sounds–Nelson, Southern North Island, Volcanic Plateau, Taranaki, Gisborne, Auckland and Northland EPs. In the South Island not extending much east of the Main Divide. Very common throughout the North Island.

Rather common in forest and scrub (60–1400 m), *Lepicolea attenuata* is an epiphyte on tree trunks and small to large branches of trees. Recorded on hosts *Nothofagus menziesii*, *N. solandri*, *Griselinia littoralis*, *Beilschmiedia tawa*, *Weinmannia racemosa*, *Halocarpus biformis*,

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Spore. 10. Portion of terminal branch with androecium toward left, dorsal view. 11. Antheridial stalk. (All from *Engel 18497*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Bealey Valley Track.)

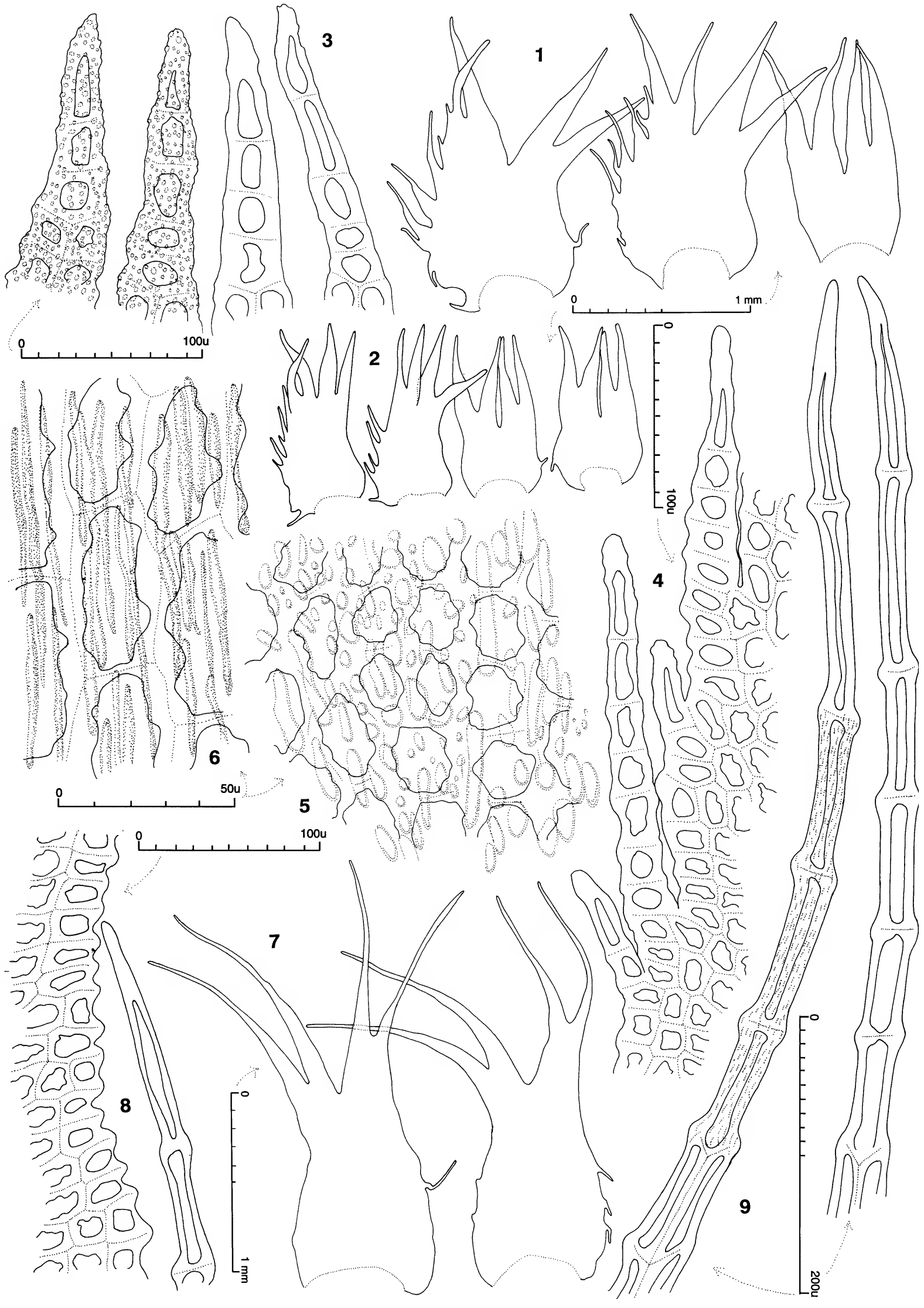

Fig. 7.
Lepicolea attenuata (Mitt.) Steph. (figs. 1–6) and *Lepicolea scolopendra* (Hook.) Dumort. *ex* Trevis. (figs. 7–9). 1. Two leaves (dorsal margin at left) and to right, an underleaf. 2. Two leaves (dor-

Lepidothamnus intermedius, *Dracophyllum longifolium* and on twigs of *Neomyrtus pedunculatus*. It may often be found loosely festooning tree branches, and on several occasions it was found on fallen tree branches, and may be a tree-top species. It also occurs on decaying logs and stumps as well as on boulders. Typical associates are *Chandonanthus squarrosus*, *Cladomnion ericoides*, *Cuspidatula monodon*, *Dicnemon calycinum*, *D. semicryptum*, *Frullania rostrata*, *Goebeliella cornigera*, *Herbertus oldfieldianus*, *Hymenophyllum armstrongii*, *Jamesoniella kirkii*, *Macromitrium longipes*, *M. microstomum*, *Paraschistochila pinnatifolia*, *P. tuloides*, *Plagiochila circinalis* and *Weymouthia cochlearifolia*.

Comments: The species may be distinguished, even in the field, by the relatively short cells of the leaf lobe apices, the cells other than the terminal cell being only at most 3:1 (Fig. 7: 3). These relatively short cells, at least for the most part, are chlorophyll-bearing and make the distal sector of the leaf lobes green and acuminate rather than hyaline and setaceous as in *Lepicolea scolopendra*.

Lepicolea scolopendra (Hook.) Dumort. *ex* Trevis.

[Plate 1E, F; Fig. 7: 7–9; Fig. 8: 2, 3, oil-bodies, p. 100]

Jungermannia scolopendra Hook., Musci Exot. 1: *pl. 40, f. 1–3.* 1818. *Sendtnera scolopendra* (Hook.) Nees *in* Gottsche, Lindenberg & Nees, Syn. Hepat. 241. 1845. *Lepicolea scolopendra* (Hook.) Dumort. *ex* Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 398. 1877. *Leperoma scolopendra* (Hook.) Bastow, Pap. & Proc. Roy. Soc. Tasmania 1887: 249. 1888. *Herbertia scolopendra* (Hook.) Kuntze, Revis. Gen. Pl. 2: 836. 1891. Type: New Zealand, South Is., Dusky Bay, 1791, *Menzies* (BM! – *c. sporo.*, FH! – *c. sporo.*).

Plants stiff and wiry, bristle-like, golden brown to pale brown; 25–65 mm long, 13–16 mm wide; shoots to 2.6 mm wide. Stems nearly covered by leaves and underleaves, rigid, wiry, lacking paraphyllia. Leaves rigid, brittle, obliquely spreading, rather densely imbricate, sub- to ± symmetrically rectangular/long-ovate to obtrapezoid, the lamina often somewhat dilated dorsally; leaves 0.60–0.95 mm wide at the level of the median sinus, 2–2.8 mm long, quadrifid, the median sinus descending to 0.6–0.85, the marginal pair of sinuses ± similar to one another in depth and shallower than the median sinus, the lobes caudate, the distal sector hyaline and setaceous, the leaf lobes with uniseriate row (420)490–630 μm long and with distinctly protuberant septa, the terminal cell 6–13:1, (130)150–200 μm long, the second and third cells from tip (2.8)3–11:1, the fourth cell 2–4:1, the segment margins entire; dorsal and ventral margins of lamina broadly curved, subauriculate at base, the marginal cells with swollen, protuberant septa giving a coarsely crenulate appearance, the dorsal margin otherwise ciliate-laciniate and with the distal sector of armature setaceous, the ventral entire or with a lacinia.

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sal margin at left) and to right, 2 underleaves. 3. Distal sectors of leaf lobes (surface detail shown for 2 lobes at left). 4. Portion of dorsal margin of leaf lamina showing armature. 5. Median cells of leaf lamina showing striate-papillose cell-wall thickenings. 6. Median-basal cells of leaf lamina showing long-striate cell-wall thickenings. 7. Leaves (dorsal margin at right). 8. Portion of dorsal margin of leaf lamina and to right, distal cells of a cilium from same margin. 9. Distal part of leaf lobes (surface ornamentation indicated at left on basal 3 cells of uniseriate row). (Figs. 1, 5–6, from type of *Sendtnera quadrifida*; 2–4, from type of *Sendtnera attenuata*; 7–9, from *Jungermannia scolopendra*.)

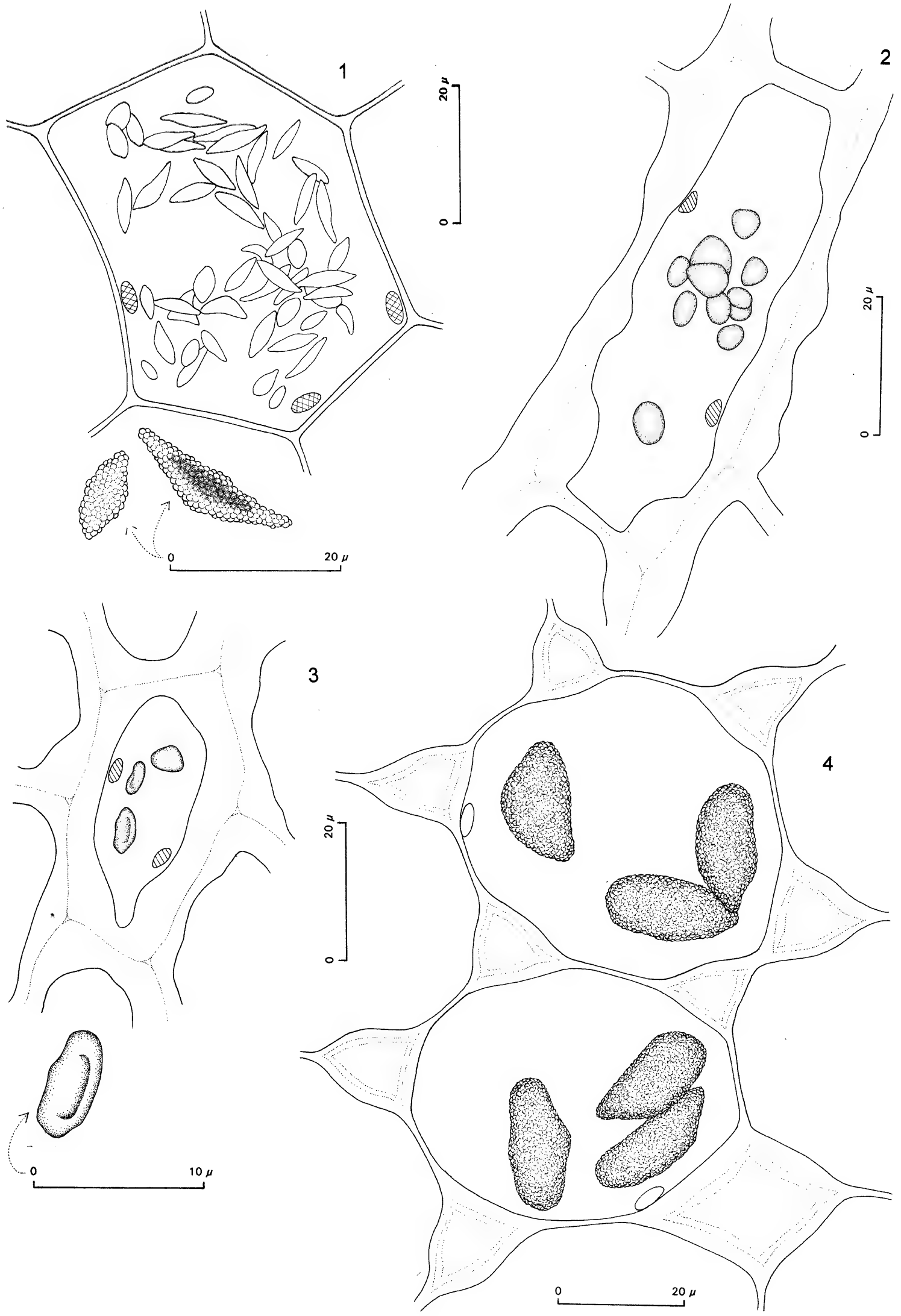

Fig. 8.
Oil-bodies. 1. *Haplomitrium gibbsiae* (Steph.) R.M.Schust. Median cells of leaf, the outline of a few chloroplasts included; below left 2 oil-bodies at higher magnification, the one at right show-

Vitta of leaves distinct, in median sector of lamina and extending to level of median sinus, or, less conspicuously, to middle of lobes, but not to the apices; cells of vitta elongate, near the leaf base 18–25 μm wide, 38–58 μm long. Leaf cells with massive trigones, the cells between vitta and margin in median sector of lamina 18–22 μm wide and long; surface of lamina striate-papillose, of uniseriate row of lobes finely striate, of leaf base markedly long-striate. Oil-bodies occupying a small portion of cell lumen, pale smokey grey, 2–4 per basal cell of lobe, 6–11 per cell at base of disc, homogeneous, subglobose to broadly elliptic, often irregularly so, sometimes subcrescentic, often with a rather elongate depression, 1.9–2.4 × 2.9–4.8 μm, globose ones 2.4–3.4 μm in diam. Underleaves ± clasping the stem, widely spreading to squarrose, the lobes often broadly reflexed, imbricate, symmetric, obtrapezoid, 2–2.1 mm long, quadrifid, the median sinus descending to 0.7–0.8; lobes as in leaves; lamina margins crenulate as in leaves, otherwide entire or repand. Asexual reproduction lacking or ?by leaf fragmentation. Fungal partner absent.

Plants dioecious. Androecia restricted to branches, wider than sterile sectors of branch, terminal but eventually becoming intercalary; bracts in 4–6 pairs, less deeply divided than leaves, the lamina ventricose and with dorsal and ventral margins ciliate. Gynoecia on short abbreviated branches; bracts of innermost series obtrapezoid, quadrifid, the median sinus descending to ca. 0.75, the lateral pair of sinuses much shallower, the lobes caudate and with uniseriate sector as in leaves, the lobe margins entire; lamina margins ciliate-laciniate, the armature setaceous distally; bracteoles of innermost series with shape and lobes as in bracts, the median sinus descending nearly to base; lamina margins sparingly dentate to ciliate. Coelocaule 2.3 mm long, 1.3 mm in diam. including cilia.

Seta to 2.8 mm long. Capsule 1 mm in diam., the wall 66–72 μm thick, of 5–6 layers; outer layer of cells subquadrate to short-rectangular, with two-phase–type thickenings, the radial walls with broad-based nodular to spur-like thickenings that tend to cluster on opposing sides of a radial wall, the thickenings very large in proportion to cell volume; innermost layer of cells with dense nodular thickenings, semiannular bands lacking.

Spores ellipsoidal, 30–35 × 24–25 μm, brown, aculeate with truncate spines ca. 5 μm long, surface with fine papillae between the spines. Elaters tortuous, 12–13 μm wide, bispiral, strongly tapered toward the tips.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, Stewart Island, South Island (0–915 m); Australia: Tasmania, Victoria; the species is absent from southern South America (Engel and Merrill, 1996b). In the South Island known from Fiordland, Westland and Western Nelson EPs. Uncommon in Nelson, and most common west of the Main Divide south of about Arthur's Pass; in Southland not known east of Fiordland.

On bryophyte-covered logs or epiphytic in lowland to montane forests of tall podocarps, *Nothofagus* and *Weinmannia*, 0–500 m. Less common in upper montane short forest and pen-

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ing an elongate depression. 2. *Lepicolea scolopendra* (Hook.) Dumort. *ex* Trevis. Basal cells of leaf, the outline of a few chloroplasts included. 3. *Lepicolea scolopendra* (Hook.) Dumort. *ex* Trevis. Median leaf cells, below an oil-body at higher magnification, the outline of a few chloroplasts included. 4. *Neogrollea notabilis* E.A.Hodgs. Median leaf cells, the outline of a few chloroplasts included; note "lamellated" or "layered" trigones. (Fig. 1, from *Glenny 9422,* New Zealand, South Is., Canterbury EP, Craigieburn Ra., Lyndon Saddle; 2, 3, from *Glenny 9594,* New Zealand, South Is. Western Nelson EP, Stockton Plateau; 4, from *Braggins JEB00401A*, New Zealand, South Is., Nelson, ca. 0.5 km from Denniston.)

alpine scrub of *Halocarpus biformis*, *Lepidothamnus intermedius*, *Metrosideros umbellata*, *Olearia colensoi*, *Phyllocladus alpinus* and *Dracophyllum* spp. (870–1000 m), as well as on rocky knolls and on slopes of mostly exposed, bare rock in areas with sparse vegetation (e.g., a few scattered shrubs and grasses at 510–570 m). Typical associates are *Acromastigum anisostomum*, *Bazzania adnexa*, *Bunodophoron* spp., *Dicnemon calycinum*, *Dicranoloma robustum*, *Gackstroemia weindorferi*, *Herbertus oldfieldianus*, *Radula buccinifera*, and at open rocky sites, *Rhacocarpus purpurascens*.

Comments: The species may be recognized, even in the field, by the bristle-like appearance due to the hyaline, setaceous leaf lobe apices. The terminal cell of the lobes, as well as the second and third cells, are markedly elongated and capillary (Fig. 7: 8, 9). The species is more commonly terrestrial than *Lepicolea attenuata*.

Suborder 2. **NEOGROLLINEAE** J.J.Engel & Braggins

Jungermanniales suborder *Neogrollineae* J.J.Engel & Braggins, J. Hattori Bot. Lab. 91: 200. 2001.

The suborder *Neogrollineae* is monotypic, based on *Neogrollea notabilis* E.A.Hodgs. of our area.

Family **NEOGROLLEACEAE** (R.M.Schust.) J.J.Engel & Braggins

Lepidoziaceae subfam. *Neogrolleoideae* R.M.Schust., Phytologia 56: 69. 1984; (cf. also Syst. Ass. Spec. Vol. 14: 73. 1979, *nom. inval.*; New Man. Bryol. 2: 1024. 1984, *nom. inval.*; *in* R.M.Schust. & J.J.Engel, J. Hattori Bot. Lab. 63: 347. 1987). *Neogrolleaceae* (R.M.Schust.) J.J.Engel & Braggins, J. Hattori Bot. Lab. 91: 195. 2001.

Neogrollea E.A.Hodgs.

Neogrollea E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 70. 1965.

Plants subjulaceous, perfectly isophyllous, the underleaves indistinguishable from leaves, erect to procumbent, developing deep reddish to reddish brown to ferrugineous pigments, markedly water-repellent. Branching common, irregular, exceedingly plastic, commonly of *Frullania* and *Acromastigum* types and leafy throughout or becoming flagelliform; *Microlepidozia*-type branches occasional, leafy throughout; ventral- and lateral-intercalary branches also present; organization into a system of creeping, stoloniform, ramified axes and erect leafy shoots absent. Stems with cortical cells not differentiated from medullary cells or a little larger, the outer tangential wall distinctly thickened, the radial walls rather thin; medullary cells with thin walls but thickened angles. Leaves and underleaves densely imbricate, vertically oriented, rather strongly spreading, the insertion transverse or at times weakly incubous, the insertion extending to the stem midline; leaves and underleaves strongly concave, suborbicular to orbicular-quadrate, the broad apices irregularly 3–4-lobulate, the lobules at times apiculate, for the most part terminating in a single cell or a uniseriate row of 2(3) cells, the tip cell frequently with a slime papilla at the summit; margins (except at immediate base) with up to 5 (rarely 7) small, sharp or blunt, irregular teeth, the teeth variable, ranging from small ones that consist

of a mere "bump" or projection of one cell or a mere uniseriate row of 2 cells to larger teeth composed of a uniseriate row of 2–3 cells subtended by a base of 2–5 cells. Cells in median sector of leaf subisodiametric, 27–38 μm wide and long, with trigones typically knot-like to nodulose, with the cell lumen often bounded mostly by the trigones, the trigones exceptionally medium and straight-sided or even a little concave; surface coarsely striate-papillose, the papillae are crowded and somewhat inconsistently distributed. Oil-bodies grey but appearing brownish in cells with pigments, 2–4 per cell, finely but prominently granular, spherical and 9–12 μm in diam. to banana-shaped, or sometimes elliptic-ovoid with acute ends, 9–10.5 × 15–22.5 μm. Fungal partner an ascomycete?

Plants dioecious. Androecia isophyllous, on short but not markedly abbreviated, slender, laxly spicate, ventral- and lateral-intercalary branches, occasionally proliferating vegetatively distally; bracts and bracteoles identical, in 3–5 gyres, ca. 0.25–0.3 the size of normal leaves and underleaves, moderately ventricose and with a 2–3(4)-lobulate apex; antheridia (1)2 per bract and bracteole, the stalk long, biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the base of gynoecium moderately swollen, with a few rhizoids; bracts of innermost series larger than leaves, suberect (but never closely sheathing the perianth) grading to squarrose-recurved, deeply concave, feebly obovate to ± obtrapezoid, 3–5-lobed; lobes narrowly acute to acuminate, composed of at most moderately elongated cells, the lobes terminating in a uniseriate row of 2(3) moderately elongated (to 4:1) cells, the lobe margins irregularly dentate by 1–2-celled teeth or by the apical end of a marginal cell diverging and forming a tooth; lamina margin bordered by cells of variable shape and orientation, irregularly dentate to sublobulate, for the most part terminating in (or consisting of) a uniseriate row of 2–4 cells, at times the apical end of a marginal cell diverging and forming a tooth; bracteole similar in size and form. Calyptra extending to ca. 0.4 the perianth length, the unfertilized archegonia near the calyptra base. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly and deeply plicate toward mouth, the perianth narrowing toward the distinctly contracted mouth; mouth ca. 12-lobulate, each lobule with 1(2) moderately thick-walled, contorted cilia and a few teeth below, the cilia composed of 2–3(5) elongate cells, the terminal cell of each cilium rounded at the summit and not sharp; perianth cells ± regularly subrectangular below mouth, the surface distinctly long-striate; perianth 3(locally 4)-stratose near base, becoming 2-stratose in median portion.

Seta long, elevating capsule well beyond perianth, with 14 rows of outer cells surrounding an inner core of ca. 27 much smaller cells. Capsule ellipsoidal, the wall 3-stratose and 38–44 μm thick to 4-stratose, and 46–52 μm thick, the inner layer subequal in thickness to intermediate layer(s) or a little thicker; outer layer of cells in surface view short-rectangular, notably thin-walled, with very imperfect two-phase development, i.e., the longitudinal walls with up to 5 large nodules (that may extend to 0.5 the cell width or a little more) alternating with walls with nodules typically sparingly developed and smaller, or, occasionally, the alternating walls devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically with an isolated nodule; innermost layer of cells markedly narrowly rectangular, the radial walls with thin, continuous sheets of wall material, the walls with semiannular bands rather common, close, sometimes incomplete, sporadically forked, the radial walls with well-developed nodule-like thickenings often present, the innermost layer with strong, irregular thickenings at the cell ends (which are so thick that the transverse walls of the inner layer are difficult to observe).

Spores 19.7–20.6 μm in diam. (including bacula), the wall amber-brown, baculate, the bacula rather closely spaced, sometimes slightly wider at base, truncate at the apex and often

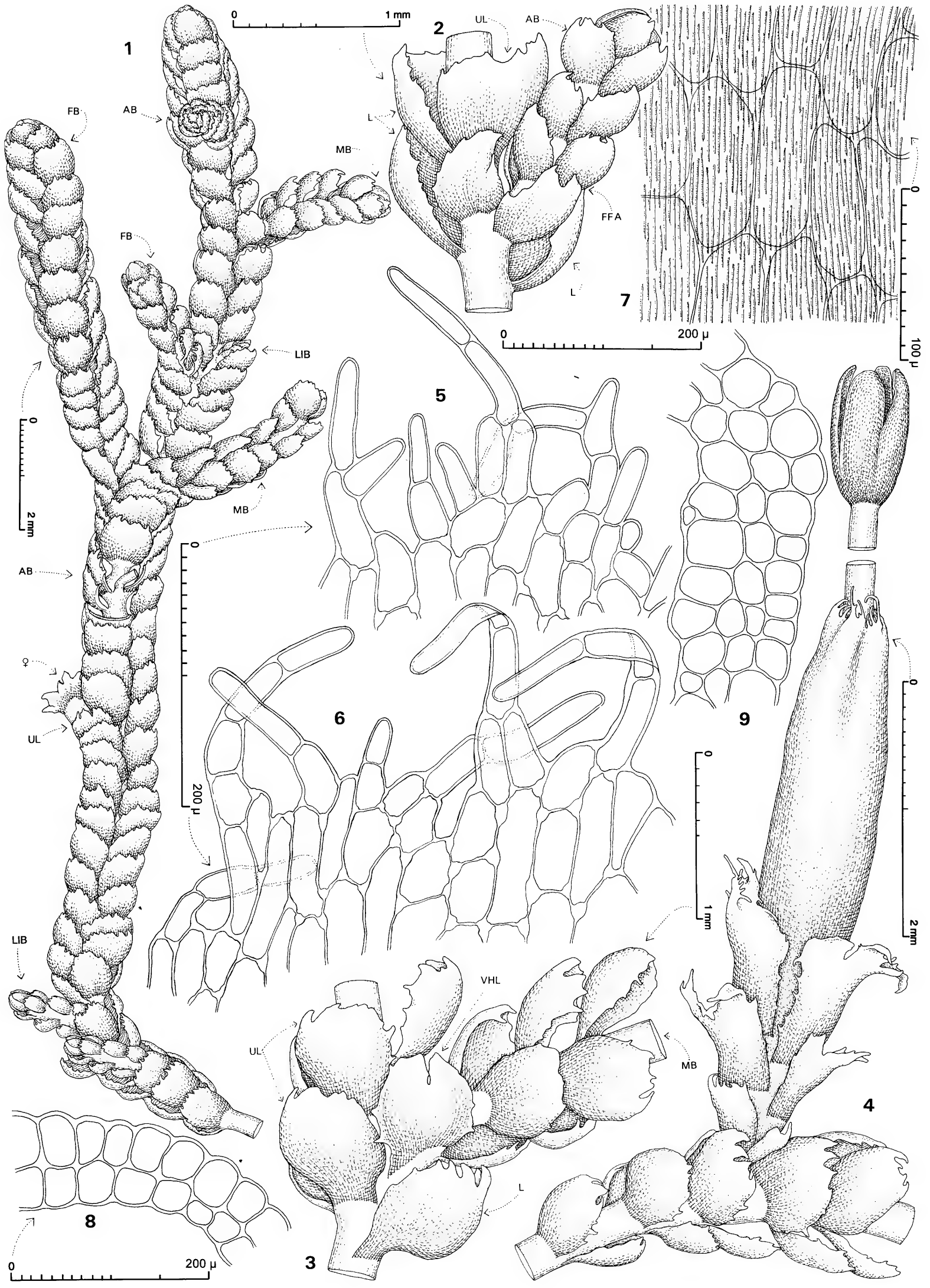

Fig. 9.
Neogrollea notabilis E.A.Hodgs. 1. Plant (ventral view) with *Frullania*-type branches (= FB), *Acromastigum*-type branches (= AB, note an underleaf removed in median sector of shoot to show

flared, the bacula sometimes irregularly joined. Elaters tortuous, 9.6–10.6 μm wide, slightly tapering toward tips, bispiral to the tips, the spirals 4.3–4.8 μm wide, closely wound.

Type: *Neogrollea notabilis* E.A.Hodgs.

References: Engel and Braggins (2001); Hodgson (1965); Schuster (1973, 1999e, 2000a).

Neogrollea notabilis E.A.Hodgs.

[Plate 2A–C; Fig. 8: 4, oil-bodies, p. 100; Figs. 9, 10]

Neogrollea notabilis E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 70. 1965. Holotype: New Zealand, South Is., Westland, 6 miles from Charleston on Westport side, *J. Taylor* (MPN ex herb. Hodgson!); isotype: (CHR 135588!).

The description of the subfamily and genus serves to characterize the species.

Distribution and Ecology: New Zealand: South Island (0–700 m); Australia: Tasmania (for comments on distribution and ecology in Tasmania see Engel and Braggins, 2001).

Neogrollea has very narrow ecological requirements throughout its range. In New Zealand the species is known almost exclusively from low-lying, waterlogged, acidic sites with poor drainage (pakihi). All stations in New Zealand are on the west coast of the South Island in Western Nelson EP within 30 km of Charleston and Westport (see map in Engel and Braggins, 2001, fig. 13). At the site north of the Big Totara River (*leg. Engel 21567*) *Neogrollea* occurred in an open *Empodisma minus – Gleichenia* bog on sandy soil; associated were *Goebelobryum unguiculatum* and *Lethocolea pansa*, with few other bryophytes. "Much of this terrain is permanently wet or submerged in 1–5 cm of water, with gradual accumulation of organic matter on wet sand. Only where the sand surfaces and relatively open areas occur, in sites where submersion is rare or nonexistent, and where desiccation never occurs, does the *Neogrollea* appear—repeatedly so" (Schuster, 1999e, p. 338). Vascular plant vegetation was not in close enough proximity to provide shade to the *Neogrollea*.

Also known from north of Tiropahi River (*Braggins 95629A*); at this station plants occurred in a pakihi swamp on the upper side of depressions at the bases of *Empodisma minus*, and in amongst low *Leptospermum scoparium*. The plants occurred on humus with *Kurzia* sp., and were shaded by taller vegetation. The Denniston population (*Braggins JEB98502A*) occurred with *Kurzia*, *Riccardia* and *Symphyogyna* on damp clay soil with *Drosera*, *Lycopodiella diffusa*, *Rhacocarpus purpurascens* and *Dicranoloma*. *Empodisma minus* is common, and the

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branch origin and half-underleaf), *Microlepidozia*-type branches (= MB), lateral-intercalary branches (= LIB), and a gynoecium (= ♀) in axil of an underleaf (= UL, only base of ♀ shown). 2. Portion of main shoot with base of *Acromastigum*-type branch (= AB); note half-underleaf, first foliar appendage (= FFA); ventral view (leaves and underleaf of main shoot indicated by L and UL respectively). 3. Portion of main shoot with base of *Microlepidozia*-type branch (= MB; VHL = ventral half-leaf; UL = underleaf; L = leaf), ventral view. 4. Portion of shoot with mature, sporophyte-bearing gynoecium on ventral-intercalary branch. 5, 6. Portions of perianth mouth (surface ornamentation not shown). 7. Outer surface of perianth (distal third) showing long striae. 8, 9. Cross sections through median and basal sectors of perianth, respectively. (All from *Braggins JEB502A*, New Zealand, South Is., Western Nelson EP, ca. 0.5 km from Denniston.)

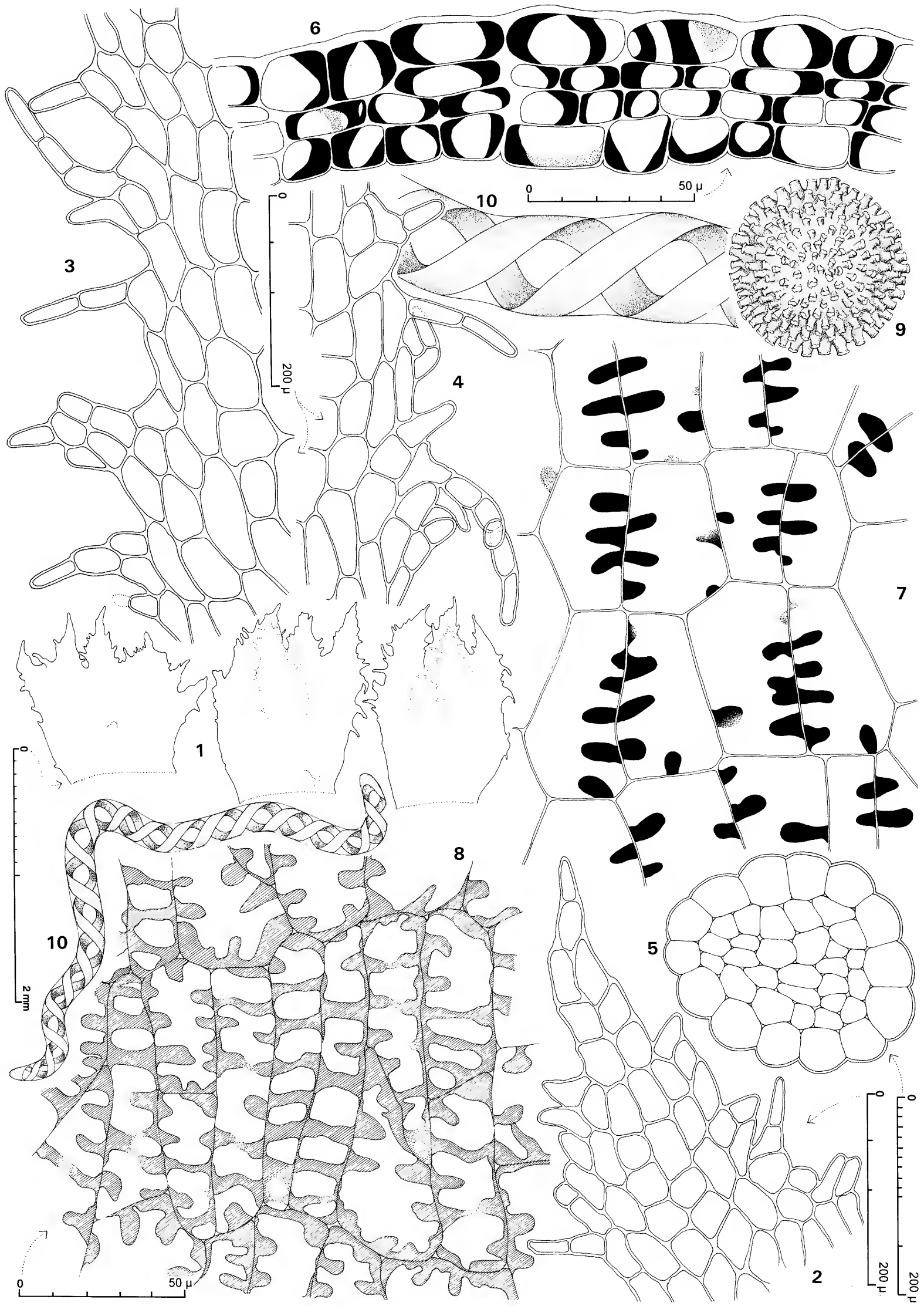

Fig. 10.
Neogrollea notabilis E.A.Hodgs. 1. Innermost bracts, and in middle, bracteole, abaxial view; note various lamellae and lobes on adaxial face shown in stipple outline. 2. Lobe of innermost ♀ bract.

site is dominated by 2–3 m tall *Leptospermum scoparium* (Engel and Braggins, 2001, fig. 14: 1). *Neogrollea* forms extensive broken patches in both exposed and shaded areas. The site may occasionally dry out somewhat (as in early Dec. 2000), but the substrate (a thin layer of organic material over a pale inorganic layer) remains moist. At Stockton Plateau (*Glenny 7535*) the species is associated with many of the same species as the Denniston site. The site, a *Gleichenia – Empodisma minus* bog, represents the highest known elevation (700 m) for the species in New Zealand.

Comments: The combination of distinctive features will distinguish *Neogrollea* from all others. The perfect isophylly on mature shoots is so marked that it is frequently very difficult to determine dorsal vs. ventral aspects. Also notable is the exceedingly plastic branching, with *Frullania*-, *Acromastigum*- and *Microlepidozia*-type terminal branches all present, together with ventral- and lateral-intercalary branches. The julaceous habit, the presence of wall pigments, the conspicuous trigones, the coarse surface ornamentation, the strongly concave, suborbicular to orbicular-quadrate leaves and underleaves with broad irregularly 3–4-lobulate apices also are useful diagnostic characters.

Suborder 3. **HERBERTINEAE** R.M.Schust.

Jungermanniales suborder *Herbertineae* R.M.Schust., J. Hattori Bot. Lab. 26: 231. 1963.

The *Herbertineae* include three regional families and, probably, also the *Grolleaceae* (Solari) R.M.Schust. of southern South America (cf. Schuster, 1973, 1984e; Solari, 1974). Recognition of families in the suborder remains controversial. For example, Schuster (1973) placed *Grollea* R.M.Schust., with only *G. antheliopsis* R.M.Schust., in the *Blepharostomataceae*, whereas Hässel (1980a) included the genus in the *Antheliaceae*, and Schuster (1984c, 2000a) placed it in its own family, *Grolleaceae*. The suborder is largely southern temperate in range; the *Trichotemnomaceae* R.M.Schust. are found only in New Zealand, and some genera (all *Trichocoleaceae*) are exclusively southern temperate, i.e., *Archeochaete* R.M.Schust. (southern South America, Falkland Islands), *Archeophylla*, *Eotrichocolea* (both New Zealand), *Herzogiaria* Fulford (southern South America) and *Isophyllaria* (Australasia, southern South America). Some genera have a number of tropical-montane representatives, e.g., *Herbertus* and *Trichocolea*, both of which also have one species each in eastern North America.

Family **HERBERTACEAE** Müll.Frib.

Herbertaceae Müll.Frib. *ex* Fulford & Hatcher, Bryologist 61: 284. 1959; R.M.Schust., Rev. Bryol. Lichénol. 26: 125. 1957. (Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland, ed. 3, 6(1): 557. 1954, *sin. descr. lat.*)

Plants subisophyllous to isophyllous, usually erect, at times pendulous, straw-colored to yellowish brown to deep brown to reddish brown; shoots medium to large and vigorous; plants

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3, 4. Portions of lamina margin of 2 innermost ♀ bracts. 5. Seta, cross section. 6. Capsule wall, cross section. 7. Capsule wall, outer layer (drawn to same scale as fig. 8). 8. Capsule wall, inner layer. 9. Spore and portion of elater at same magnification (× 1382). 10. Elater (× 468). (All from *Braggins JEB502A*, New Zealand, South Is., Western Nelson EP, ca. 0.5 km from Denniston.)

with a weakly to strongly developed system of basal, prostrate, rhizomatous stolons from which arise upright leafy shoots, the leafy shoots, in turn, forming geotropic, stoloniform branches. Branching sparing, irregular, predominantly ventral-intercalary, less often lateral-intercalary; *Frullania*-like branches rare and sporadic. Stems with cortex weakly to strongly differentiated, thick-walled, typically smaller than the medullary cells. Rhizoids typically restricted to stolons, at underleaf bases and, at times, from underleaves (less often from leaves), the rhizoids also at times on basal sectors of upright leafy shoots but rarely in distal sectors. Leaves with insertion weakly incubous, often subtransversely oriented, often ventrally secund and often ± falcate, ± symmetric to rather asymmetric, short-bifid (*Olgantha*) or 2–3(4)-lobed to 0.4–0.8 or more, the lobes acute to lanceolate, entire; lamina margins entire or with a few teeth or short cilia at the base. Cells evenly thick-walled or with strongly nodulose, often confluent trigones; cells in median to basal sector often elongated, at times forming a vitta that extends to varying degrees distally; striate-papillose. Oil-bodies (*fide* Schuster, 2000a) usually 6–12 or more per cell, homogeneous (*Herbertus*) or finely botryoidal (*Triandrophyllum*). Underleaves transversely inserted, symmetrical, with shape and form much as in leaves. Asexual reproduction lacking or some species of *Herbertus* with fragmenting leaves (1 sp. with caducous leaves).

Dioecious. Androecia isophyllous, terminal on leading leafy shoots, becoming intercalary; bracts similar to leaves but pouched at base, with 2–4(6) antheridia; bracteoles like the bracts, with antheridia; antheridial stalk long, 2(4)-seriate. Gynoecia isophyllous, terminal on leading leafy shoots; bracts and bracteoles ensheathing the perianth, similar to one another and basically with shape and form like those of leaves and underleaves but often with more teeth. Perianth ovate to elliptic, deeply plicate, the mouth deeply divided into 6–9 lobes ± similar to those of the leaves.

Seta massive, of numerous cells. Capsule subspherical or spherical, the wall 4–9-layered; outer layer of cells with one-phase ontogeny, with nodular thickenings; inner layer with semi-annular bands.

Spores papillose or granular-vermiculate or with truncated tubercles, ca. 2–2.5× the elaters in diam. Elaters 2(3)-spiral.

Three genera belong here. Two, *Triandrophyllum* and *Herbertus*, have representatives in the southern temperate region, while the third does not. *Olgantha* R.M.Schust. (Schuster, 1996c) has only *O. eophylla* R.M.Schust., a plant from the hyperparamo of Ecuador (4200–4300 m).

Herbertus Gray

Herbertus Gray, Nat. Arr. Brit. Pl. 1: 678, 705. 1821.
Schisma Dumort., Commentat. Bot. 114. 1822. *Mastigophora* sect. *Schisma* Nees, Naturgesch. Eur. Leberm. 3: 573. 1838.
Sendtnera Endl., Gen. Plant., Suppl. 1: 1342. 1840.
Herpocladium Mitt. *in* Seem., Fl. Vit. 405. 1873 (1871).

Plants green to more often stramineous brown to deeply reddish brown, the leafy stems small to robust, often with the facies of a moss, ranging from 2 up to 25 cm long; plants at times developing a system of basal, prostrate, rhizomatous, microphyllous stolons from which arise ascending to erect (often pendulous in epiphytic species), typically unbranched, leafy shoots. Branching ventral-intercalary, very rarely lateral-intercalary. Stems rigid, brittle, the

cortex well differentiated, in 2–4 layers of thick-walled cells each often with a reduced lumen; medullary cells thinner-walled, becoming gradually larger in diameter toward the median sector. Rhizoids typically on stoloniform axes, usually originating from cells of underleaves and, sporadically, leaves, rarely near bases of leafy shoots. Leaves often falcate, often somewhat ventrally secund, asymmetric, bifid to 0.4–0.8 (rarely asymmetrically 3-fid in a few taxa), the lobes subequal or the dorsal slightly larger, the lobes narrowly acute-lanceolate to acuminate-lanceolate, entire; lamina margins entire or with several slime papillae and, at times, teeth terminating in a slime papilla. Cells with trigones strongly nodulose, often confluent, vittate: with a median-basal field of elongate-rectangular cells extending into the lobes (frequently to the lobe tips), the marginal and submarginal cells ± isodiametric; surface striate-papillose. Oil-bodies up to 20–24 per vitta cell, glistening, homogeneous, smooth. Underleaves at times slightly smaller than leaves, transversely inserted, symmetric, typically ± squarrose, not falcate, the lobes ± parallel to slightly divergent.

Dioecious. Androecia wider than sterile sectors of shoot, typically with 4–8 pairs of bracts, subspicate; bracts and bracteoles similar to leaves and underleaves in form but pouched at the base, typically less deeply bifid and with lamina margins more toothed, both bracts and bracteoles with 2–3 antheridia. Gynoecia with bracts and bracteoles in 3–4 series, the innermost series much larger than leaves, deeply bifid, the lamina margins (and at times the basal sector of the lobes) denticulate-dentate. Perianth plicate, the mouth divided to 0.3–0.5 into 6 lobes similar to those of the leaves, with each alternate sinus somewhat more deeply descending; lobe margins (and at times also the inner surface) often dentate, with numerous slime papillae.

Seta of numerous cells. Capsule subspherical, with 4 valves, but occasionally with secondary, irregular splitting into additional valves, the wall 5–9-layered.

Spores with truncated tubercles, ca. 2–2.5× the elaters in diam. Elaters 2–3-spiraled.

Type: *Herbertus aduncus* (Dicks.) Gray (≡ *Jungermannia adunca* Dicks.)

Herbertus has ca. 25 species (Gradstein et al., 2001) and is widespread in montane, subalpine and alpine regions. A few species occur in the Northern Hemisphere, e.g., western Europe, Appalachia, western North America (including Arctic Alaska), but the genus is more predominantly in tropical regions. Ten species, for example, occur in tropical America (Gradstein et al., 2001), and eight species occur in Australasia and the South Pacific (So, 2003b). The genus is not well represented in southern temperate and subantarctic regions. One species, *H. runcinatus* (Taylor) Kuntze, is found in southern South America and Juan Fernandez (Hässel and Solari, 1976; Engel, 1978), and one occurs in New Zealand and Tasmania.

References: Hodgson (1967; *H. alpina*); So (2003b); Stewart (1978; oil-body data of *H. alpina*; Schuster, 2000a).

Herbertus oldfieldianus (Steph.) Rodway

[Plate 2D; Figs. 11, 12; Fig. 13: 1, 2, oil-bodies, p. 114]

Schisma oldfieldianum Steph., Sp. Hepat. 4: 19. 1909. *Herbertus oldfieldianus* (Steph.) Rodway, Tasman. Bryoph. 2: 72. 1916. Type: Australia, Tasmania, *Oldfield s.n.* (G!); isotype: (FH!).

Schisma alpinum Steph., Sp. Hepat. 4: 20. 1909. *Herberta alpina* (Steph.) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 185. 1967. Type: New Zealand, W side of Ruahine Ra. *Colenso 5179* (G!, WELT 7619!).

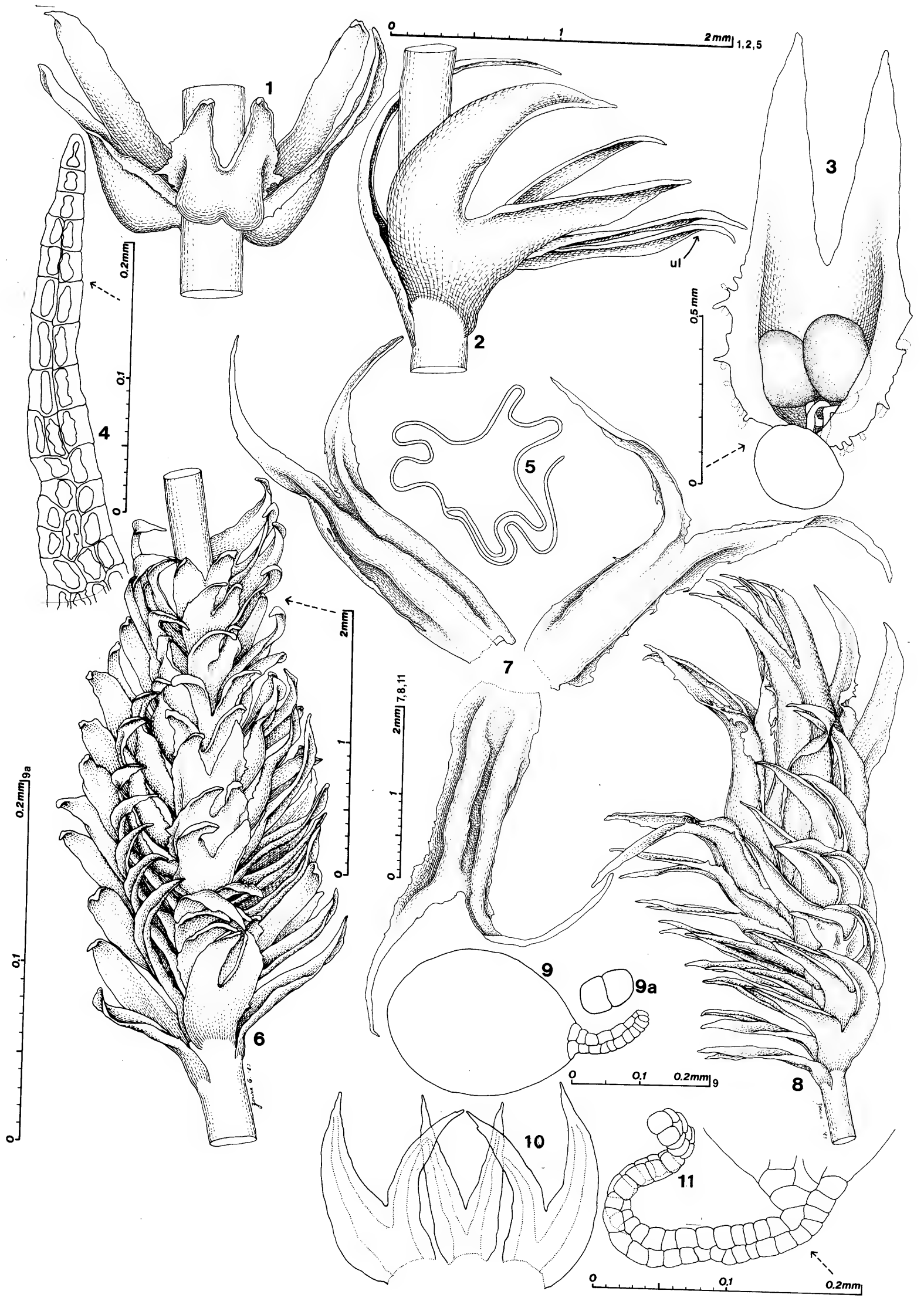

Fig. 11.
Herbertus oldfieldianus (Steph.) Rodway. 1. Sector of androecium showing antheridial-bearing bracteole and bracts, ventral view. 2. Two opposing leaves and adjacent underleaf (= ul). 3. ♂

Plants often forming compact tufts, stiff, olive-green to yellow-brown, at times tinged with red-brown, with a system of branched, geotropic and plagiotropic stolons and microphyllous axes from which arise erect, leafy shoots that are often feebly cernuous at the tips; shoots 20–40 mm long, to 2 mm wide, the older parts of the shoots often bare of leaves. Branches of leafy shoots common, ventral-intercalary, often stoloniform, often initially small-leaved and soon becoming flagelliform. Leaves rigid, ventrally secund, imbricate, the insertions overlapping dorsally, the dorsal bases of opposing leaves distinctly overlapping and covering stem in dorsal view, divided to 0.65–0.75, 0.50–0.8 mm wide at the lobe bases, 0.6–1.05 mm wide between the lobe apices, 1.3–1.8 mm long; lobes falcate, 2.9–4.8× longer than wide, convex toward base (sometimes strongly so on the dorsal side), the distal sector (especially of ventral lobe) concave-channeled, the tip often apiculate, terminating in a single cell or a uniseriate row of 2–5 cells; lamina convex, the margins inflexed, with several sessile slime papillae; vitta of leaves distinct, extending nearly to lobe apices. Leaf cells with trigones massive, the marginal and submarginal cells of lamina 17–22 μm wide, 11–18 μm long, the intramarginal cells becoming gradually larger as the vitta is approached; vitta cells near leaf base with transverse radial walls very thin, the cells 22–25 μm wide, 50–70 μm long; lobe tip surfaces rather distinctly striate-papillose, of disc obscurely so. Oil-bodies appearing rather crowded in vitta cells, in non-vitta cells occupying only moderate portion of cell, pale smokey grey or hyaline and glistening, 13–15 per vitta cell, those in vitta cells globose to narrowly to broadly elliptic, occasionally sublinear, 4 × 4 μm to 3 × 7 μm; oil-bodies in nonvittate cells 3–6 per cell, 1.5–3 × 2.5–4 μm; oil-bodies breaking up by way of tiny spherules that swell from the oil-body surface. Underleaves similar in size and form to leaves but not secund, widely spreading to squarrose, oblong-elliptic to cuneate; lobes ± parallel to somewhat diverging; lamina margins abruptly incurved, the several slime papillae sessile or with a unicellular stalk. Asexual reproduction lacking or ?by fragmenting leaves and ♀ bracts. Fungal partner absent.

Androecia on main shoot, wider than sterile sectors of shoot; bracts more closely imbricate than leaves, in 4–6 pairs, the lobes falcate, the bracts and bracteoles less deeply lobed than leaves, the lamina distinctly ventricose, the lamina margins irregularly denticulate, at times sparingly so, the margins with sessile slime papillae. Gynoecia sporadic, on main shoot; bracts and bracteoles similar (except bract lobes feebly falcate), forming a compact and "bud-like" structure, those of innermost series with at least the basal sector appressed to and ensheathing perianth, divided to ca. 0.5 by caudate lobes, the lamina deeply concave, the shape of the concavity(ies) conforming to the shape of perianth plicae, margins of lamina and lower sectors of lobes with spinose teeth and copious sessile and stalked slime papillae, the stalks + spinose teeth rendering the margins irregularly denticulate-dentate. Perianth barely exserted beyond bracts, 3.2–4.1 mm long, 1.2–1.3 mm in diam., ± elliptic, basically trigonous but each angle with 2 lobes, divided to the middle into 6 caudate lobes ca. 1.5 mm long, the lobe margins denticulate-dentate and with copious slime papillae.

Bracteole with 2 antheridia. 4. Portion of perianth mouth. 5. Perianth, cross section through median third. 6. Shoot with androecium (swollen zone), ventral view (note basal, saccate portion of bracts and bracteoles). 7. ♀ Bracts and (lower) bracteole from innermost series. 8. Perianth bearing shoot. 9. Antheridium (with only distal portion of stalk); the stalk (a) at higher magnification. 10. Two leaves and between, an underleaf from one gyre (flattened), the boundary of vittae indicated. 11. Antheridial stalk. (Figs. 1–11, from *Engel 14021B*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park, Ballroom Forest.)

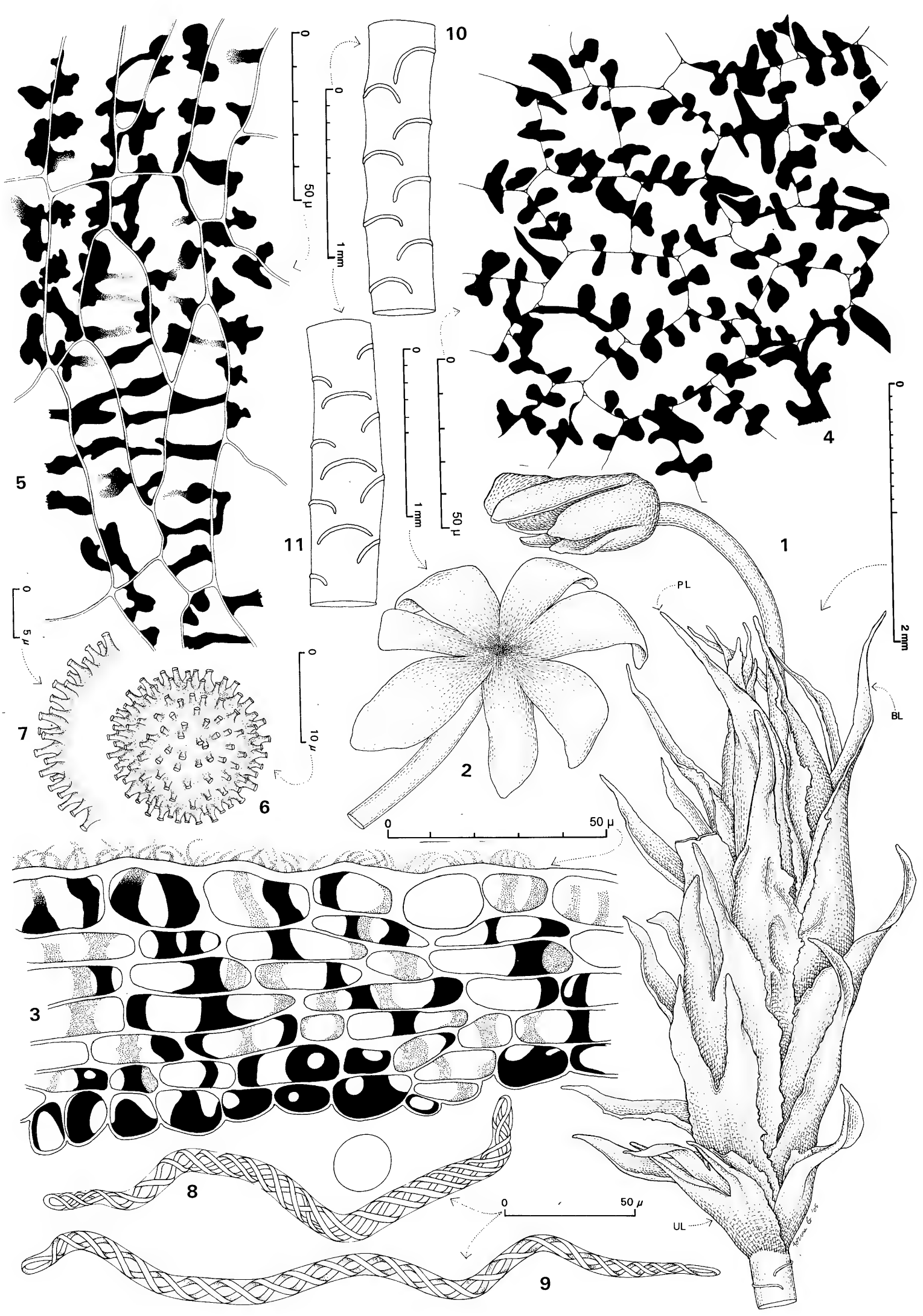

Fig. 12.
Herbertus oldfieldianus (Steph.) Rodway. 1. Gynoecium with sporophyte, ventral-lateral view (UL = underleaf). Note secondary splitting of valves and (below) overlapping underleaf and leaf insertions. Note the strong isophylly of gynoecium and gradual transition of leaves and underleaves

Seta ca. 3.2 mm long. Capsule splitting longitudinally but unevenly, the wall 6–8-layered and 48–60 μm thick to 8–9-layered and 86–90(100) μm thick (Schuster, 2000a), the outer layer of cells equal to thickness of slightly over 2 of interior strata; outer layer of cells densely covered with an amorphous, ± granular, waxy substance (soluble in xylene), irregular in shape, subquadrate to irregularly short-rectangular, the radial walls firm, hyaline, with red-brown, strongly nodular thickenings on both longitudinal and transverse walls, the thickenings often appearing "stalked," the nodules rather irregular in shape, some with a notch at the summit, some attenuated and spine-like, most pigmented, a few hyaline, a few band-like thickenings present at the cell ends or edges; innermost layer of cells irregularly narrowly elongate-rectangular, the radial walls with nodular thickenings common, occasionally with semiannular bands.

Spores 19.2–20.6 μm in diam., reddish brown, tuberculate-baculate, the tubercles truncate and often dilated at the summit, the ground surface between tubercles appearing smooth. Elaters in number adhering by one end to inner face of capsule, feebly tortuous to nearly straight, 9.6–10.6 μm wide, 3–4-spiral in median portion, bispiral and considerably more loosely wound toward ends, the spirals 2.4–2.9 μm wide; elaters at times bispiral throughout.

Distribution and Ecology: New Zealand: Campbell Island, Stewart Island, South Island (440–1540 m), North Island (960–1330 m); Australia: Tasmania. In New Zealand known from Fiordland, Otago (Mt. Cargill, Garvie Mtns.), Canterbury (Arthur's Pass, Governors Bush), Westland, Western Nelson, Sounds–Nelson (Mt. Stokes, Mt. Richmond), Southern North Island (Ruahine Ra., Tararua Ra.), Volcanic Plateau, Taranaki (Mt. Taranaki), Gisborne and Auckland (Coromandel Peninsula) EPs. The northern limit is at Mt. Moehau on Coromandel Peninsula. In the South Island, common west of and on the Main Divide but not extending far to the east.

A plant chiefly of upper montane forest and scrub of *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *Archeria traversii*, *Dracophyllum traversii*, *D. longifolium*, *D. rosmarinifolium*, and *Olearia colensoi* where it is usually epiphytic on hosts that include *N. menziesii*, *N. solandri*, *Halocarpus bidwillii* and *Weinmannia racemosa*, and is particularly common on *Archeria traversii*. It is also found on soil and rock under forest and scrub. It forms large, compact tufts on tree bases and may be locally abundant and crowded in such situations and form polsters. It also occurs in open sites on ledges and crevices of rocky (often granite) outcrops, boulder faces and steep slopes in the penalpine and alpine zones. It also occurs on damp, shady banks and on rocky knolls of slopes of mostly exposed, bare rock in areas with sparse vegetation (e.g., consisting of a few scattered shrubs and grasses). *Herbertus oldfieldianus* may occur near sea level (e.g., at Milford Sound). It is often found with *Acrobolbus cinerascens*, *Anastrophyllum schismoides*, *Dicranoloma billardierei*, *Goebeliella cornigera*, *Jamesoniella colorata*, *Leifidium tenerum*, *Lepicolea attenuata*, *L. scolopendra*, *Lepyrodon australis*, *Para-*

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with bracts and bracteoles, respectively. Note also the similarity of innermost bract lobes (= BL) with perianth lobes (= PL), the fragmentation of some lobes as well as an entire leaf (only the base shown of second leaf from base at right). 2. Dehisced capsule showing secondary splitting into supplementary valves. 3. Capsule wall, cross section, the exposed wall with an irregular waxy deposit. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. 6. Spore. 7. Spore profile showing baculae somewhat dilated at the tips. 8. Elater in part with 3 spirals; note adjacent spore profile. 9. Bispiral elater. 10, 11. Sectors of stem showing insertion lines, the dorsal view at top and, lower, the ventral view. (All from *Engel 22863*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Bealey Valley track.)

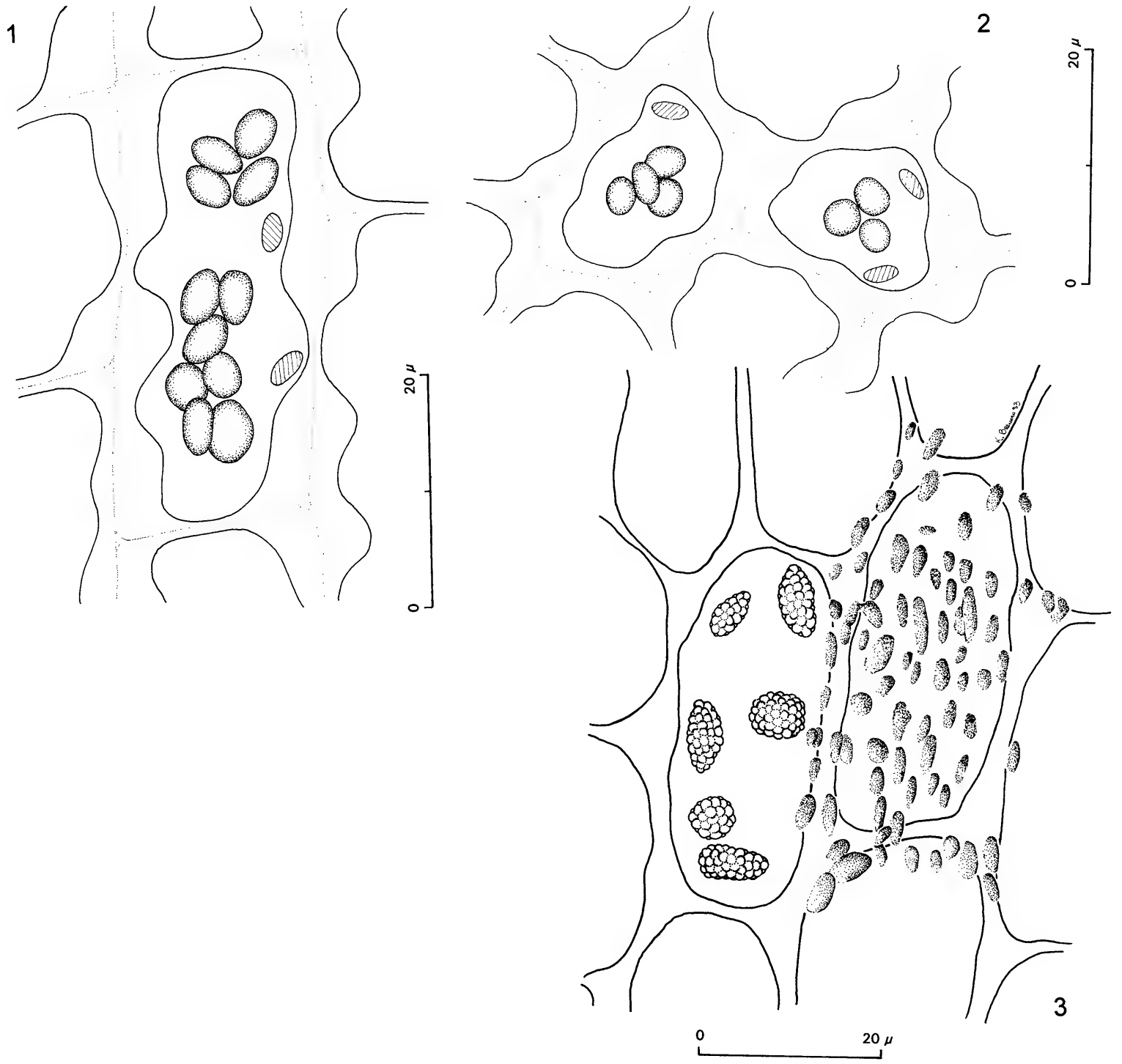

Fig. 13.
Oil-bodies. 1. *Herbertus oldfieldianus* (Steph.) Rodway. Vitta cell of upper disk, the outline of a few chloroplasts included. 2. *Herbertus oldfieldianus* (Steph.) Rodway. Non-vitta cells of leaf, the outline of a few chloroplasts included. 3. *Triandrophyllum subtrifidum* (Hook.f. & Taylor) Fulford & Hatcher. Median cells of lamina, the cell at right showing surface ornamentation. (Figs. 1, 2, from *Glenny 9211*, New Zealand, South Is., Canterbury EP, Arthur's Pass, Bealey R., Chasm track; 3, from *Glenny 8851*, New Zealand, South Is., Canterbury EP, Arthur's Pass, McGrath Creek.)

schistochila pinnatifolia, *P. tuloides*, *Plagiochila circinalis*, *Plagiochilion conjugatum* and *Radula pseudoscripta*, and, when on rock, with *Acrolophozia pectinata*, *Andreaea acutifolia*, *Cheilolejeunea campbelliensis*, *Frullania aterrima*, *Jamesoniella colorata* and *Rhacocarpus purpurascens*.

Comments: Large, fuscous or olive-brown phases typically form tufts or cushions, often extensive and pure; such plants may be many centimeters tall and have secund shoot apices, much as in the moss *Dicranoloma*. With the three rather dense series of deeply bifid leaves,

the shoots have a distinctly moss-like aspect—the long-tapered leaf lobes simulating leaves of a moss. Such plants copiously produce slender, often whip-like, frequently ramified, chiefly geotropic flagellae that simulate a root system.

By contrast, alpine/penalpine phases may be much more compact, only 1–2 cm tall × 1.2–1.5 mm wide with the leaves; such phases may be reddish brown in exposed sites, dense-leaved, with lateral leaves only weakly falcate and with less acuminate lobes. These plants have scarcely secund shoot apices and may also closely mimic mosses.

Similar to *Triandrophyllum*, especially the very stunted forms found on exposed rock. The leaves are more imbricate and less spreading from the stem, the stems are wiry and often bare of leaves at their base. Also similar to *Lepicolea* and *Dendromastigophora*, but the branching is not pinnate and branches are at a very narrow angle rather than at right angles to the stem as they are in those two genera. The cushion-forming habit of the species, whether epiphytic or terrestrial, is distinctive, as are the secund leaves, a common feature of mosses, but rarely seen in liverworts.

Triandrophyllum Fulford & Hatcher

Triandrophyllum Fulford & Hatcher, Bryologist 64: 349. 1962 (1961); Fulford & Hatcher, Bryologist 61: 277. 1959 (1958), *nom. inval. sin. gen. typ.*; Grolle, Bryologist 64: 25. 1961, *nom. inval.*

Plants strongly ascending to erect, the shoot tips straight or (often) decurved, olive-green to brown to yellow-brown, the tips at times tinged with magenta or rose, the plants medium in size. Branches rather common, irregular, of ventral- and lateral-intercalary types, originating from median and lower sectors of shoots, becoming erect and leafy or horizontal and stoloniform, the plants with a system of basal, prostrate stolons from which arise upright leafy shoots; *Frullania*-type branches rare. Stems with cortex 1(2) layers of moderately thick-walled cells about the same size as or somewhat smaller than those of the medulla; medullary cells thin. Rhizoids mostly on stoloniform branches, originating from leaf and underleaf cells, not from stem cells. Leaves rigid, obliquely spreading, obscurely ventrally secund to more distinctly so, the insertion incubous and feebly recurved at dorsal end, the leaves concave to ± canaliculate, rather asymmetric (± symmetric in *Triandrophyllum symmetricum*), quadrate to more often ovate to ovate-elliptic, often ± falcate, the dorsal margin longer, more strongly arched, dilated at the ± cordate base, the leaves 2–3(4)-lobed to 0.3–0.55; lobes unequal, the dorsal larger or (*T. symmetricum*) subequal, the lobes acute to acuminate, often apiculate, entire. Cells with walls firm and for the most part evenly thick-walled, with trigones mostly indistinct and small to at most medium (at times large and slightly bulging in *T. symmetricum*); surfaces densely striolate-papillose. Oil-bodies (see Schuster, 2000a) finely botryoidal, (1)5–12(15) per cell. Underleaves transversely inserted, slightly to moderately smaller than leaves but never less than 0.55 their size, obliquely spreading to squarrose, symmetrical, for the most part oblong-elliptical to narrowly ovate, at times subquadrate to broad ovate, 2–3(rarely 4)-lobed. Asexual reproduction absent.

Androecia with bracts and bracteoles similar to leaves and underleaves in form but pouched at the base; antheridia 2–4 in each bract and bracteole, the stalk biseriate. Gynoecial bracts of innermost series much larger than leaves but basically similar in form to them except the margins often with stronger teeth; bracteoles of innermost series similar to bracts. Perianth not demonstrably exserted beyond bracts, oblong-ovate to ovate, distinctly plicate in distal half or

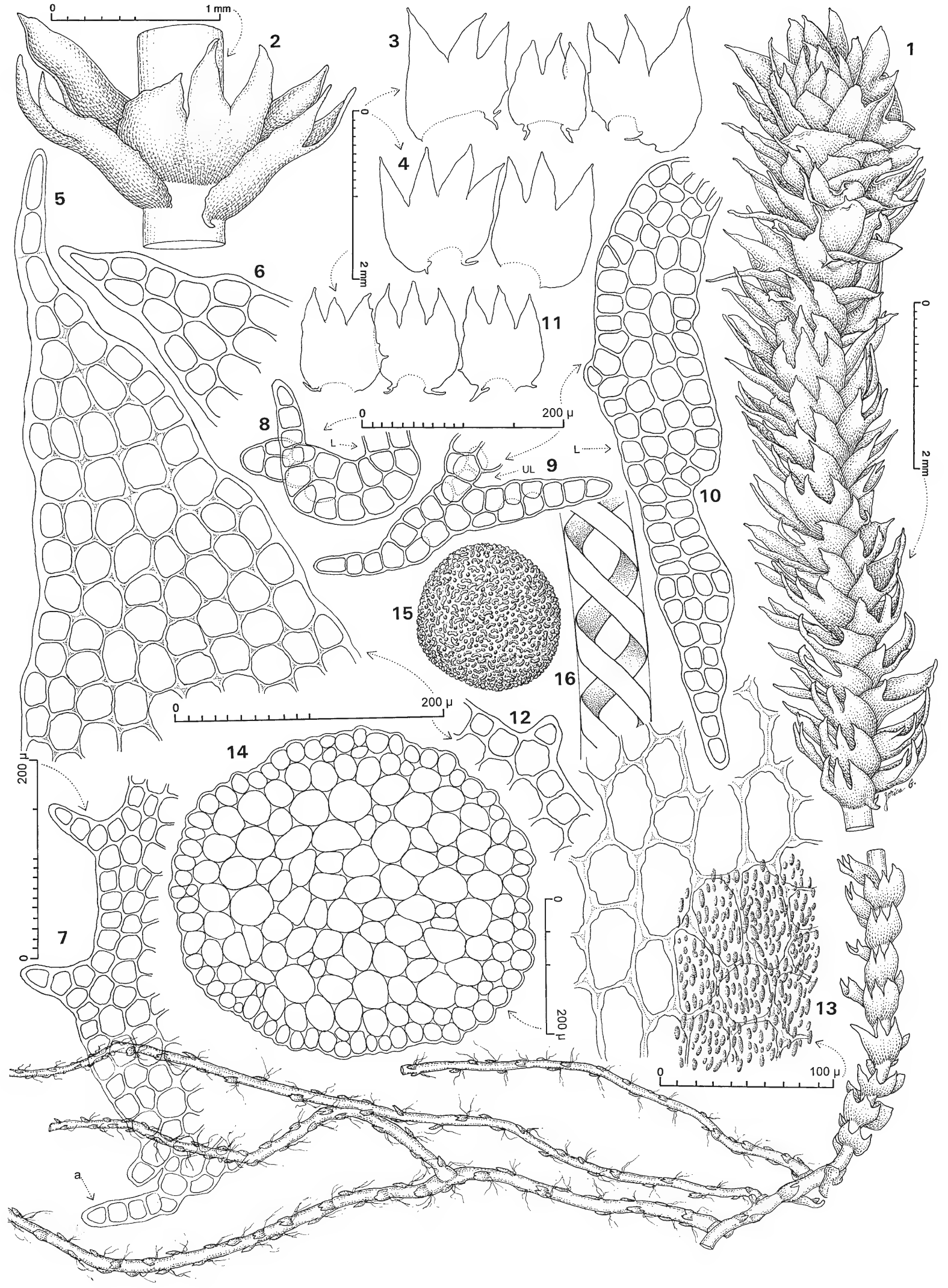

Fig. 14.
Triandrophyllum symmetricum J.J.Engel. 1. Shoot with basal, horizontal, leafless stolons, ventral view. 2. Two leaves and an underleaf, ventral view. 3. Two leaves and, in middle, an underleaf (flattened). 4. Two leaves (flattened). 5. Lobe of leaf. 6. Portion of middle lobe of leaf (drawn at same scale as fig. 5). 7. Ventral margin of leaf showing 3 teeth and, at base, an appendage (= a). 8–10.

more, the mouth divided up to 0.5 by 6–9 long and slender lobes, the lobes entire or with several teeth or cilia at the base.

Seta massive, the outer cells in up to 60 rows. Capsule ± spherical, the wall 4–6(7)-layered, the outer layer with nodular thickenings on longitudinal and transverse walls, but with scattered, longitudinal and transverse walls devoid of thickenings, the walls lacking thickenings not in any pattern; inner layer with semiannular bands.

Spores papillose-vermiculate. Elaters bispiral.

Type: *Triandrophyllum subtrifidum* (Hook.f. & Taylor) Fulford & Taylor (≡ *Jungermannia subtrifida* Hook.f. & Taylor)

The genus *Triandrophyllum* consists of four species: a) *T. subtrifidum*, which is amphi-Pacific temperate, occurring on Macquarie Island, New Zealand, Tasmania, the Philippines (Kitagawa, 1981), Tristan da Cunha, South Sandwich Islands, South Georgia, Falkland Islands, southern South America, southeastern Brazil, the Andes and Central America northward to Mexico; b) *T. symmetricum* (Engel, 1999c) of New Zealand; c) *T. fernandeziense* (S.W.Arnell) Fulford & Hatcher, endemic to Juan Fernandez Islands; and d) *T. heterophyllum* (Steph.) Grolle of New Guinea and Java. *Triandrophyllum georgiense* (Steph.) Fulford & Hatcher of South Georgia belongs in the synonymy of *T. subtrifidum* (see Solari, 1973); the species was accepted by Schuster (2000a). Gradstein (Gradstein et al., 2001) placed *Olgantha eophyllum* in *Triandrophyllum*; the species should be maintained in the monotypic *Olgantha*.

References: Engel (1999c); Fulford (1963b); Fulford and Hatcher (1959); Schuster (2000a); Solari (1973); Stewart (1978; oil-body data of *T. subtrifidum*).

Key to Species

1a. Leaves and underleaves distant to approximate, oriented at ± right angles to the stem, which is nearly always visible at least in ventral view; leaves and underleaves 2- or occasionally 3-lobed, never 4-lobed; leaves asymmetrically ovate to oblong-ovate to subrectangular, the lamina higher, 24–34 cells high from dorsal sinus base to leaf base; shoot tips decurved, the leaves and underleaves not forming a capitulum . . . . . *T. subtrifidum* (p. 120)

1b. Leaves obliquely spreading, so densely imbricate that the stem is not visible in dorsal or ventral views; leaves and underleaves 3(rarely 4)-lobed, never bilobed (even in isolated cases); leaves ± symmetric to at most weakly asymmetrically subquadrate to very short-subrectangular, the lamina shorter, 20–23 cells from dorsal sinus base to leaf base; shoot tips straight, consisting of closely imbricate leaves and underleaves that form a loose capitulum . . . . . *T. symmetricum* (p. 119)

Appendages of leaf (= L) and underleaf (= UL) bases. 11. Underleaves. 12. Tooth of underleaf lobe. 13. Median leaf cells, surface detail shown in part. 14. Seta, cross section. 15, 16. Spore and portion of elater drawn at same scale (× 1225). (All from type.)

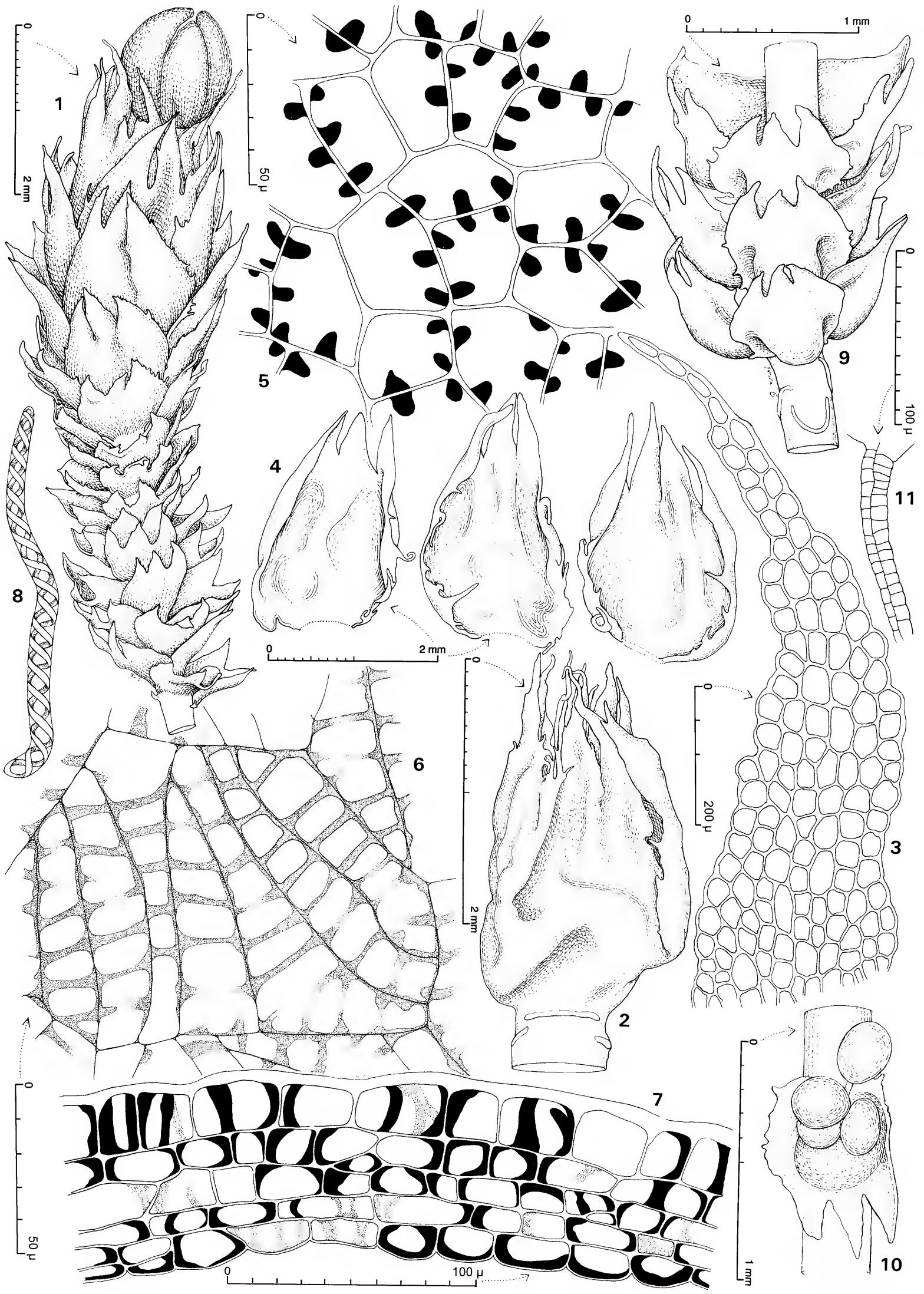

Fig. 15.
Triandrophyllum symmetricum J.J.Engel. 1. Gynoecium with mature sporophyte, ventral view. 2. Perianth (bracts and bracteole removed), ventral view. 3. Lobe of perianth mouth. 4. Innermost ♀

Triandrophyllum symmetricum J.J.Engel

[Figs. 14, 15]

Triandrophyllum symmetricum J.J.Engel, Haussknechtia Beih. 9: 115. f. 1, 2. 1999. Holotype: New Zealand, North Is., Hawkins Hill, Wellington, 7 Sept. 1981, *T. Moss s.n.* (AK); isotype (fragment): (F).

Plants erect, pale olive-green, often tinged with rose, particularly at shoot tips, the shoot tips straight and not decurved, consisting of closely imbricate leaves and underleaves, forming a loose capitulum; shoots to 2.4 mm wide. Branches rather common, of ventral- and lateral-intercalary types, originating from median and lower sectors of shoots, becoming erect and leafy or horizontal and stoloniform, the plants with a system of basal, prostrate stolons from which arise upright leafy shoots. Stems with cortex of 1 layer of cells, the exposed cell wall distinctly thickened, the cells somewhat smaller than those of the medulla; medullary cells thin. Leaves rigid, obscurely ventrally secund, obliquely spreading, closely imbricate, the stem hidden dorsally and ventrally, the insertion feebly recurved at dorsal end, the leaves concave, ± symmetric to feebly asymmetrically quadrate to very short-rectangular, about as wide as long (less than 1.1× longer than wide), consistently 3(4)-lobed to 0.45–0.55, 1.2–1.3 mm wide × 1.2–1.4 mm long; lobes subequal or the dorsal larger and the median and ventral lobes subequal in size, slightly to distinctly concave, acute, often apiculate, the tip terminating in a single cell or at most a uniseriate row of 3 thick-walled, at most slightly elongated cells, the lobe margins for the most part entire but occasionally with a tooth; lamina ca. 20–23 cells from dorsal sinus base to leaf base; dorsal margin dilated at the base, ± cordate; dorsal and ventral margins of lamina often with 1(2) appendages at extreme base, the appendages irregular, often laciniiform to lobuliform, often hook-like, the dorsal margin of lamina otherwise entire, the ventral often with 1–4 teeth. Leaf cells with walls somewhat thickened, trigones distinct, medium to large and slightly bulging, median cells of lamina 24–32 μm wide, 36–46 μm long; oil-bodies unknown; leaf surfaces densely striolate-papillose. Underleaves slightly smaller than leaves, obliquely spreading, convex (ventral view), symmetrically subquadrate to broad ovate, consistently 3-lobed to 0.4–0.5; lobes as in leaves except the tip occasionally terminating in 2 laterally juxtaposed cells and the margins more often with a tooth; margins each often with an appendage at extreme base similar to that of leaves, the margins otherwise entire or with a few teeth.

Androecia on main shoot, terminal but eventually becoming intercalary, a little wider than sterile sectors; bracts and bracteoles a little more closely imbricate than leaves and underleaves, in 4–5 pairs; bracts and bracteoles similar to leaves and underleaves except less deeply lobed, the lamina distinctly ventricose, the lamina margins with several coarse teeth; antheridia 3–4 per bract and bracteole, the stalk long (to 17 cells long). Gynoecia on main shoot or leading branches; bracts of innermost series much larger than leaves, erect, ensheathing and conforming to contours of perianth, not or feebly ventrally secund, ± symmetrically ovate, ± symmetrically 3–4-lobed (the dorsal lobe not larger), the lobes slenderly attenuate,

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bracts, and in middle, bracteole (adaxial view). 5. Capsule wall, outer layer. 6. Capsule wall, inner layer. 7. Capsule wall, cross section. 8. Elater (× 425). 9. Portion of main shoot with 3 gyres of antheridia-bearing bracts and bracteoles, ventral view. 10. ♂ Bracteole with 4 antheridia, ventral view. 11. Antheridial stalk. (All from type.)

entire; dorsal and ventral margins of lamina with to 3 or more coarse teeth, the dorsal margin at times entire, the extreme base of both margins with a conspicuous appendage; bracteoles of innermost series similar to bracts in size, shape and depth of sinuses, the lamina margins with several laciniiform to lobuliform processes. Perianth not demonstrably exserted beyond bracts, short, broadly ovate, distinctly plicate, with several plicae extending to base (at least dorsally), the perianth narrowing to the 9-lobed mouth, the lobes long, slender and often parallel-sided for much of their length, entire or with several teeth or long cilia toward base.

Seta with ca. 60 rows of outer cells surrounding an inner core of scattered, considerably larger cells. Capsule ± spherical, the wall 71–76 μm thick, of 5–6 layers; outer layer of cells ± equal in thickness of ca. 2 of intermediate layers; outer layer of cells subquadrate to short-rectangular, the radial walls with (1)2–3 red-brown, large, nodular thickenings on longitudinal and transverse walls, but with scattered, rather frequent, longitudinal and transverse walls devoid of thickenings, the walls that lack thickenings not in any pattern; innermost layer of cells irregularly elongate-rectangular, the radial walls with somewhat thick, continuous sheets of red-brown wall material, the walls with semiannular bands common and typically complete, narrow, sometimes forked.

Spores 17.3–18.2 μm in diam., reddish brown, with low, sharply defined, close, irregular, short, sometimes furcate, vermiculate ridges and, often, papillae. Elaters straight or feebly tortuous, 9.6–10.1 μm wide, bispiral, the spirals 3.4–3.8 μm wide, rather closely wound, extending to the tips.

Distribution and Ecology: New Zealand: North Island (435 m). Known only from the type, which is from Hawkins Hill (41° 19′ S, 174° 44′ E), near Wellington, at ± 435 m in a steep-sided stream gully with *Hymenophyllum minimum*. Plants of this species were not found in a search of this area in 2003.

Comments: This species differs from *Triandrophyllum subtrifidum* in a number of respects, including aspect, leaf orientation and symmetry. Shoot tips are straight, consisting of closely imbricate leaves and underleaves, and form a loose capitulum. On the other hand, shoot tips of *T. subtrifidum* are recurved and never form a capitulum. Leaves and underleaves of *T. symmetricum* are obliquely spreading and are so densely imbricate that the stem is not visible in either dorsal or ventral views (Fig. 14: 1; Fig. 15: 1) vs. leaves and underleaves that are oriented at ± right angles to the stem and distant to approximate so that the stem is nearly always visible at least in ventral aspect in *T. subtrifidum* (Fig. 16: 1). Leaves of *T. symmetricum* are 3(rarely 4)-lobed and ± symmetric to at most weakly asymmetric (Fig. 14: 3, 4) vs. 2–3-lobed and distinctly asymmetric in *T. subtrifidum* (Fig. 16: 3, 4). Also, *T. symmetricum* has deeper leaf sinuses: 20–23 cells from dorsal sinus base to leaf base vs. 24–34 cells high in *T. subtrifidum*.

Triandrophyllum subtrifidum (Hook.f. & Taylor) Fulford & Hatcher

[Plate 2E, F; Fig. 13: 3, oil-bodies, p. 114; Fig. 16]

Jungermannia subtrifida Hook.f. & Taylor, London J. Bot. 3: 579. 1844. *Isotachis subtrifida* (Hook.f. & Taylor) Mitt. *in* Hook.f., Bot. Antarc. Voy. 2(2): 149. 1854. *Mastigophora subtrifida* (Hook.f. & Taylor) E.A.Hodgs., Rev. Bryol. Lichénol. 18: 25. 1949. *Triandrophyllum subtrifidum* (Hook.f. & Taylor) Fulford & Hatcher, Bryologist 64: 350. 1962 (1961). Type: Tasmania, *Hooker* (S!).

Plate 1

A *Haplomitrium gibbsiae*, distal sector of shoots, male plant (left) and female plant with capsule (right). Photo, W. Malcolm.

B *Haplomitrium gibbsiae*, female plants showing archegonia. Photo, J. Braggins.

C *Haplomitrium gibbsiae*, male plants showing antheridia. Photo, J. Braggins.

D *Lepicolea attenuata*, habit, showing coelocaules. Photo, J. Braggins.

E *Lepicolea scolopendra*, habit, showing bristle-like texture and pinnate branching. Photo, J. Braggins.

F *Lepicolea scolopendra*, shoot apex. Photo, W. Malcolm.

Plate 2

A *Neogrollea notabilis*, habit. Photo, J. Braggins.

B *Neogrollea notabilis*, perianth and sporophyte. Photo, J. Braggins.

C *Neogrollea notabilis*, ventral (left) and dorsal (right) views of the same shoot showing isophyllous condition. Photo, W. Malcolm.

D *Herbertus oldfieldianus*, habit. Photo, W. Malcolm.

E *Triandrophyllum subtrifidum*, covering soil bank; note long setae. Photo, J. Braggins.

F *Triandrophyllum subtrifidum*, habit; note decurved shoot tips. Photo, W. Malcolm.

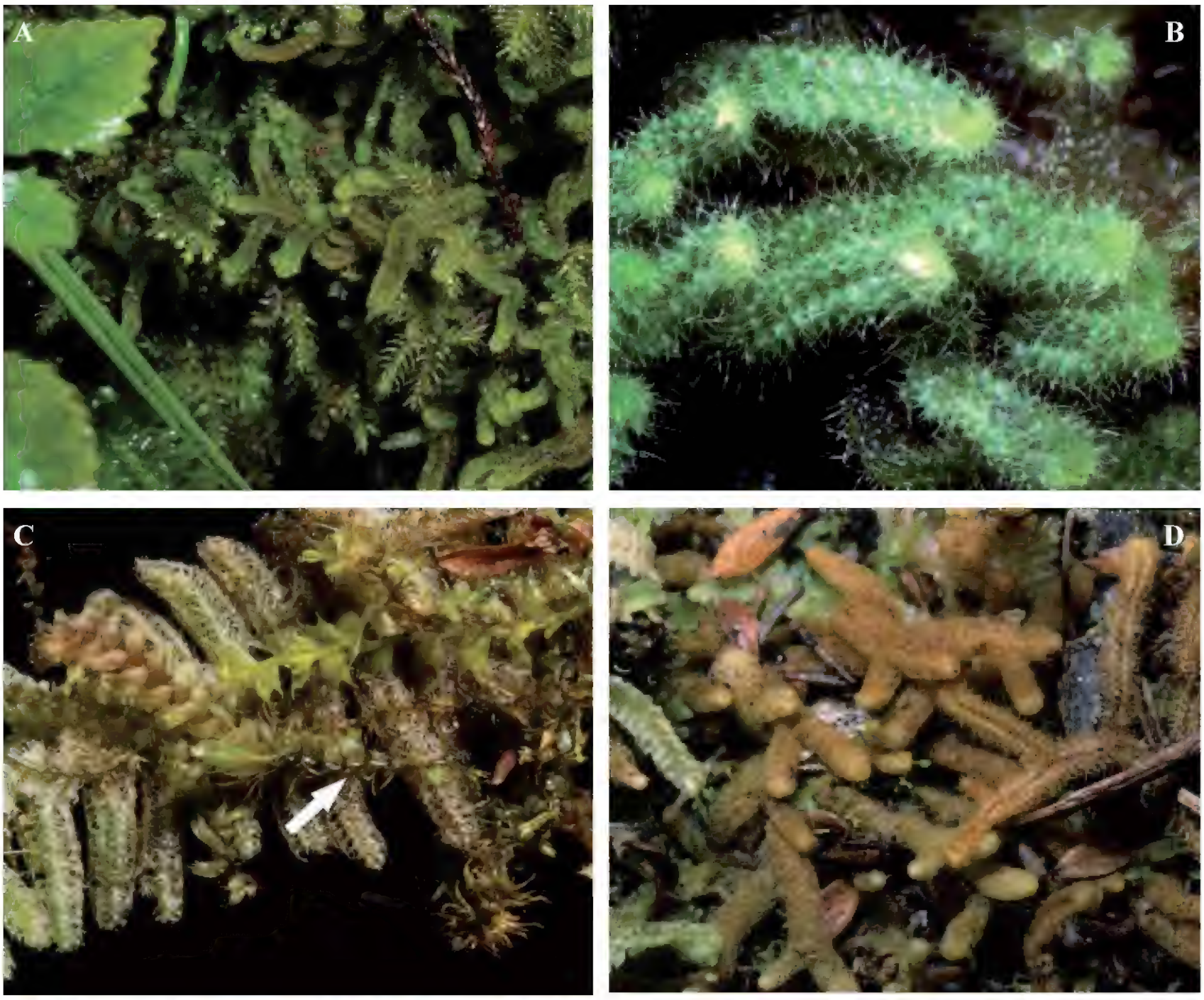


Plate 3

A *Temnoma pulchellum*, habit. Photo, J. Braggins.

B *Temnoma pulchellum*, habit. Photo, W. Malcolm.

C *Archeophylla schusteri*, growing on *Herzogianthus vaginatus*, with *Acrobolbus lophocoleoides* and *Clandarium xiphophyllum.* Arrow points to the *Archeophylla.* Photo, J. Braggins.

D *Castanoclobos julaceus*, habit. Photo, J. Braggins.

E *Castanoclobos julaceus*, habit. Photo, J. Braggins.

F *Leiomitra lanata*, habit, showing coelocaules and elongate seta of sporophyte. Photo, J. Braggins.

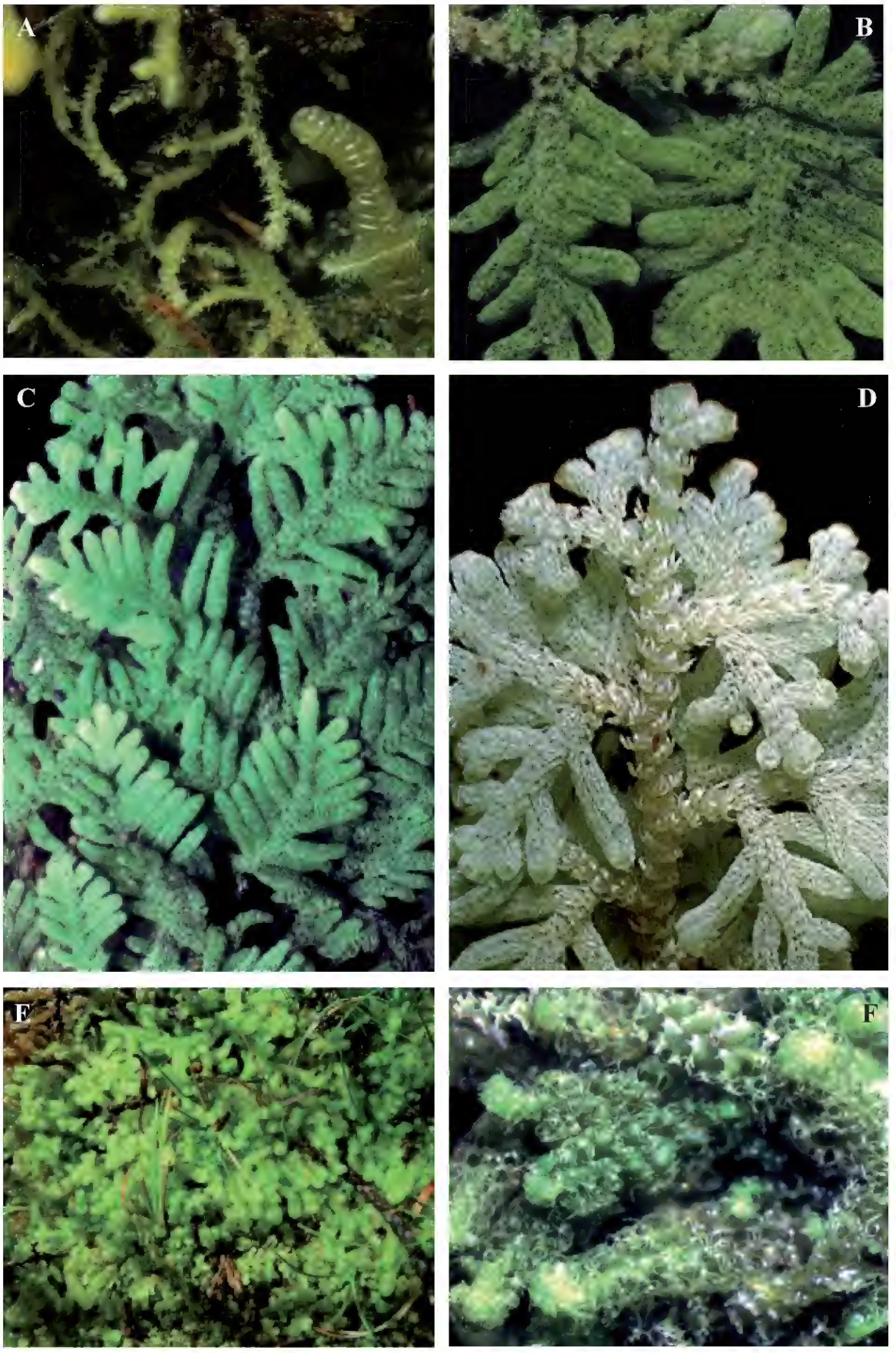


Plate 4

A *Eotrichocolea polyacantha*, habit. Photo, J. Braggins.
B *Trichocolea mollissima*, showing details of two branches. Photo, J. Braggins.
C *Trichocolea hatcheri*, habit. Photo, W. Malcolm.
D *Trichocolea mollissima*, distal sector of plant showing 2–3-pinnate branching. Photo, W. Malcolm.
E *Trichotemnoma corrugatum*, habit. Photo, M. von Konrat.
F *Trichotemnoma corrugatum*, habit. Photo, W. Malcolm.

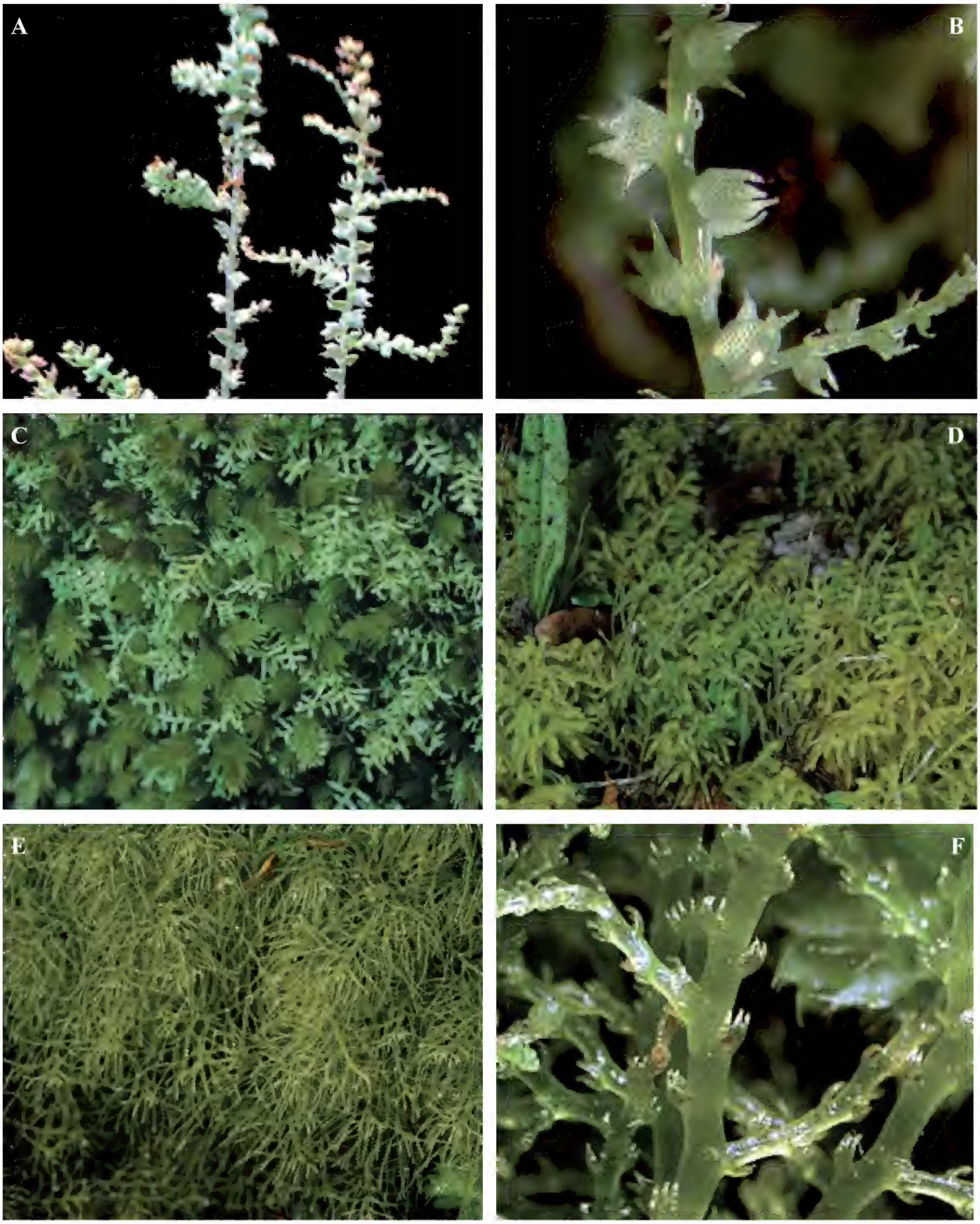


Plate 5

A *Lepidozia digitata*, two shoots. Photo, W. Malcolm.
B *Lepidozia digitata*, shoot detail. Photo, W. Malcolm.
C *Lepidozia glaucescens*, habit, among *Leucobryum candidum.* Photo, J. Braggins.
D *Lepidozia pendulina*, habit; note small capsules on long slender setae. Photo, J. Braggins.
E *Lepidozia microphylla*, habit. Photo, J. Braggins.
F *Lepidozia microphylla*, shoot detail. Photo, W. Malcolm.

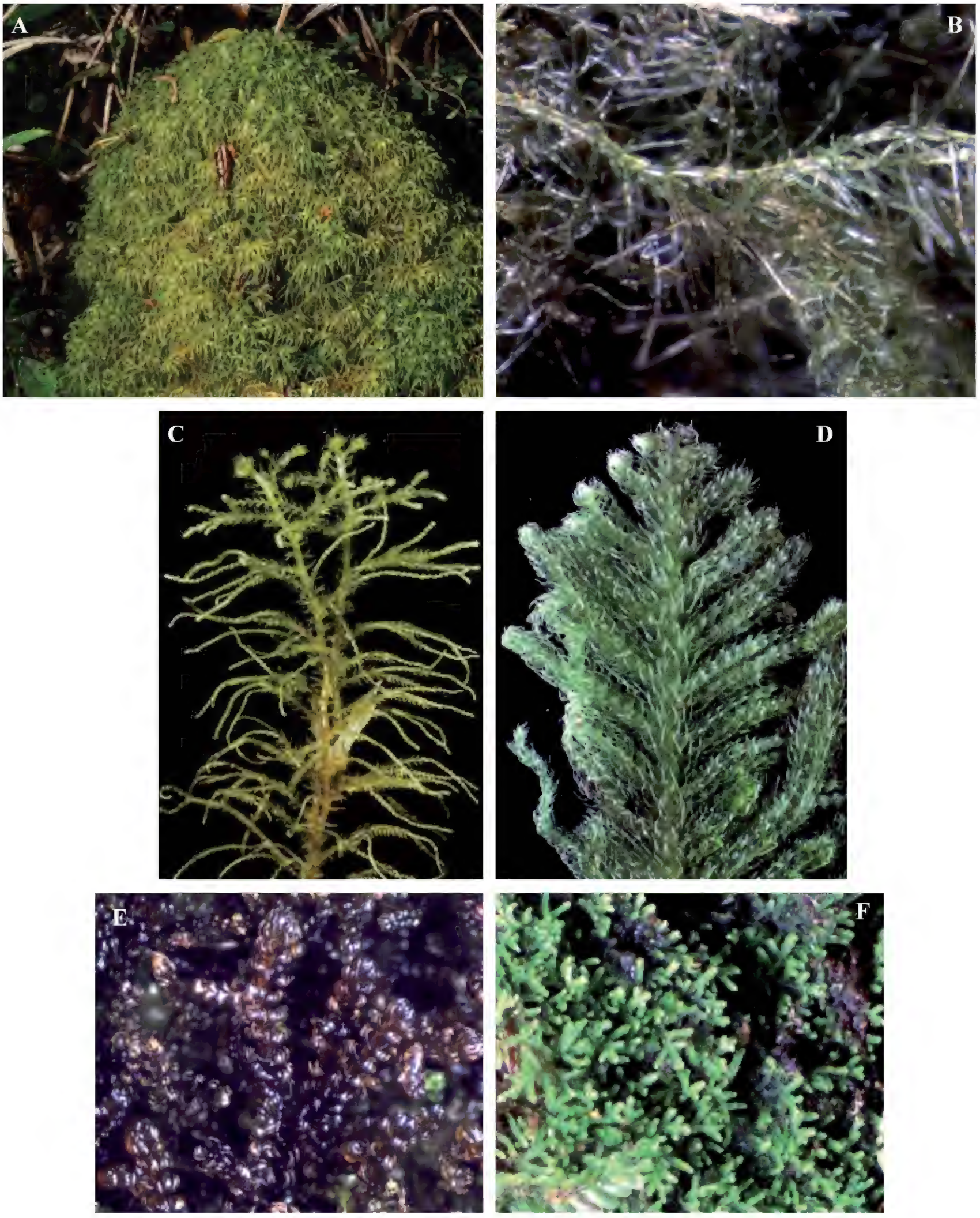


Plate 6

A *Lepidozia spinosissima*, ± pure hummock on forest floor. Photo, J. Braggins.
B *Telaranea herzogii*, habit. Photo, W. Malcolm.
C *Lepidozia spinosissima*, whole plant with perianth. Photo, J. Braggins.
D *Telaranea gibbsiana*, distal sector of shoot. Photo, W. Malcolm.
E *Kurzia helophila*, habit; note pigmentation. Photo, W. Malcolm.
F *Kurzia hippuroides*, habit. Photo, W. Malcolm.

Plate 7

A *Psiloclada clandestina*, habit. Photo, W. Malcolm.
B *Psiloclada clandestina*, main shoot with branches. Photo, W. Malcolm.
C *Drucella integristipula*, habit; note capsule (upper middle). Photo, J. Braggins.
D *Acromastigum anisostomum*, habit. Photo, W. Malcolm.
E *Bazzania novae-zelandiae*, habit. Photo, J. Braggins.
F *Bazzania novae-zelandiae*, close-up of shoots. Photo, W. Malcolm.

Plate 8

A *Bazzania tayloriana*, habit; note glaucous condition. Photo, W. Malcolm.

B *Bazzania involuta*, showing intercalary stoloniform branches and dominance of leading shoots. Photo, W. Malcolm.

C *Zoopsis nitida*, habit, growing on damp rotten wood on lower side of old fallen tree trunk. Photo, J. Braggins.

D *Pseudocephalozia lepidozioides*, habit. Photo, J. Braggins.

E *Zoopsidella caledonica*, whole plants on humus; note leaf areolation visible at lower magnification. Photo, W. Malcolm.

F *Zoopsidella caledonica*, single leaf. Photo, W. Malcolm.

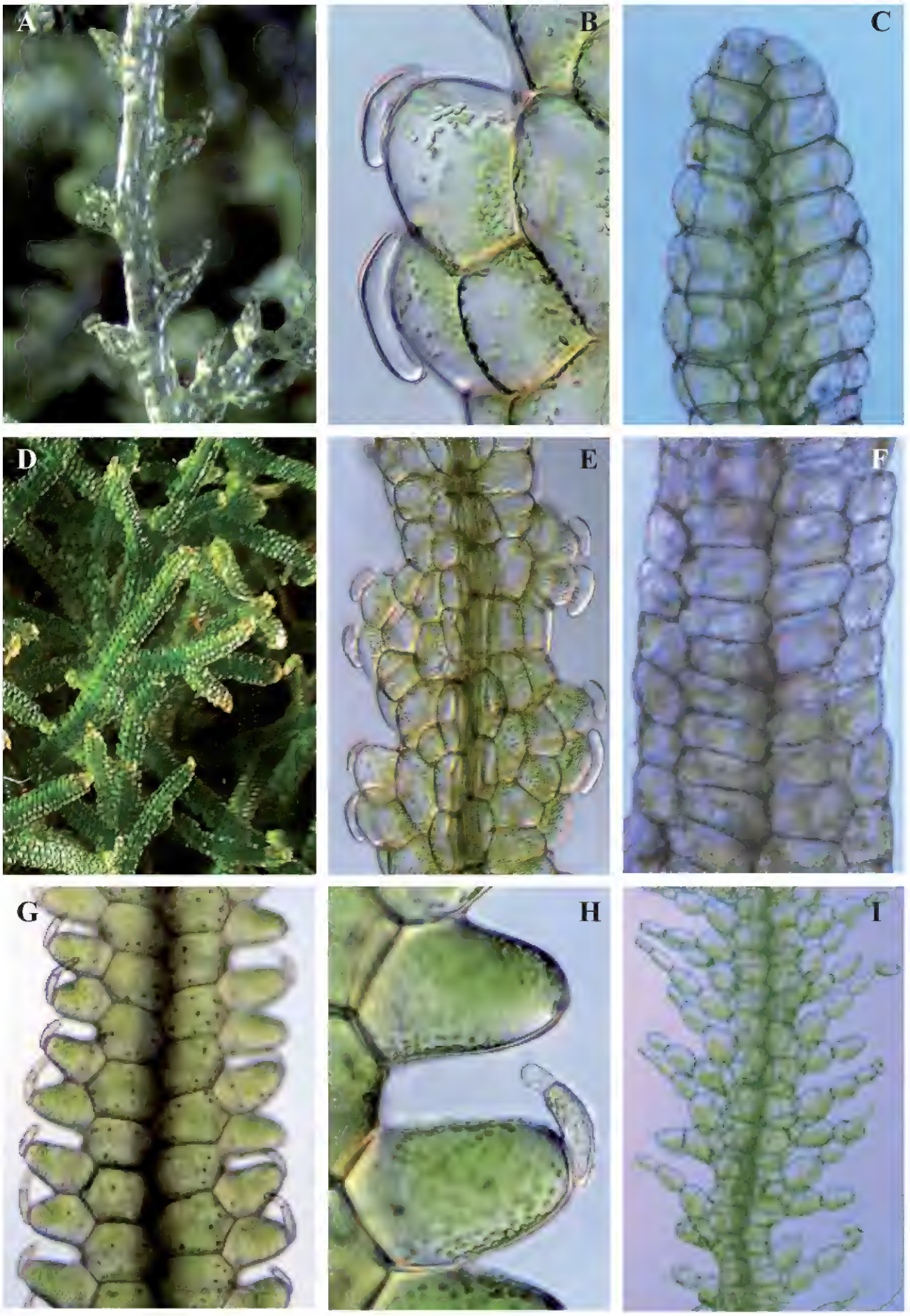


Plate 9

A *Zoopsis leitgebiana*, single shoot. Photo, W. Malcolm.
B *Zoopsis argentea*, margin of shoot showing reduced leaves, dorsal view. Photo, W. Malcolm.
C *Zoopsis bicruris*, leading shoot showing reduced leaves (at right) and medullary strand. Photo, D. Glenny.
D *Zoopsis setulosa*, view of whole plants. Photo, W. Malcolm.
E *Zoopsis argentea*, shoot, dorsal view, showing reduced leaves and medullary strand. Photo, W. Malcolm.
F *Zoopsis nitida*, dorsal view of shoot. Photo, D. Glenny.
G *Zoopsis setulosa*, dorsal view of shoot. Photo, W. Malcolm.
H *Zoopsis setulosa*, margin of shoot showing reduced leaf. Photo, W. Malcolm.
I *Zoopsis matawaia*, dorsal view of shoot. Photo, D. Glenny.

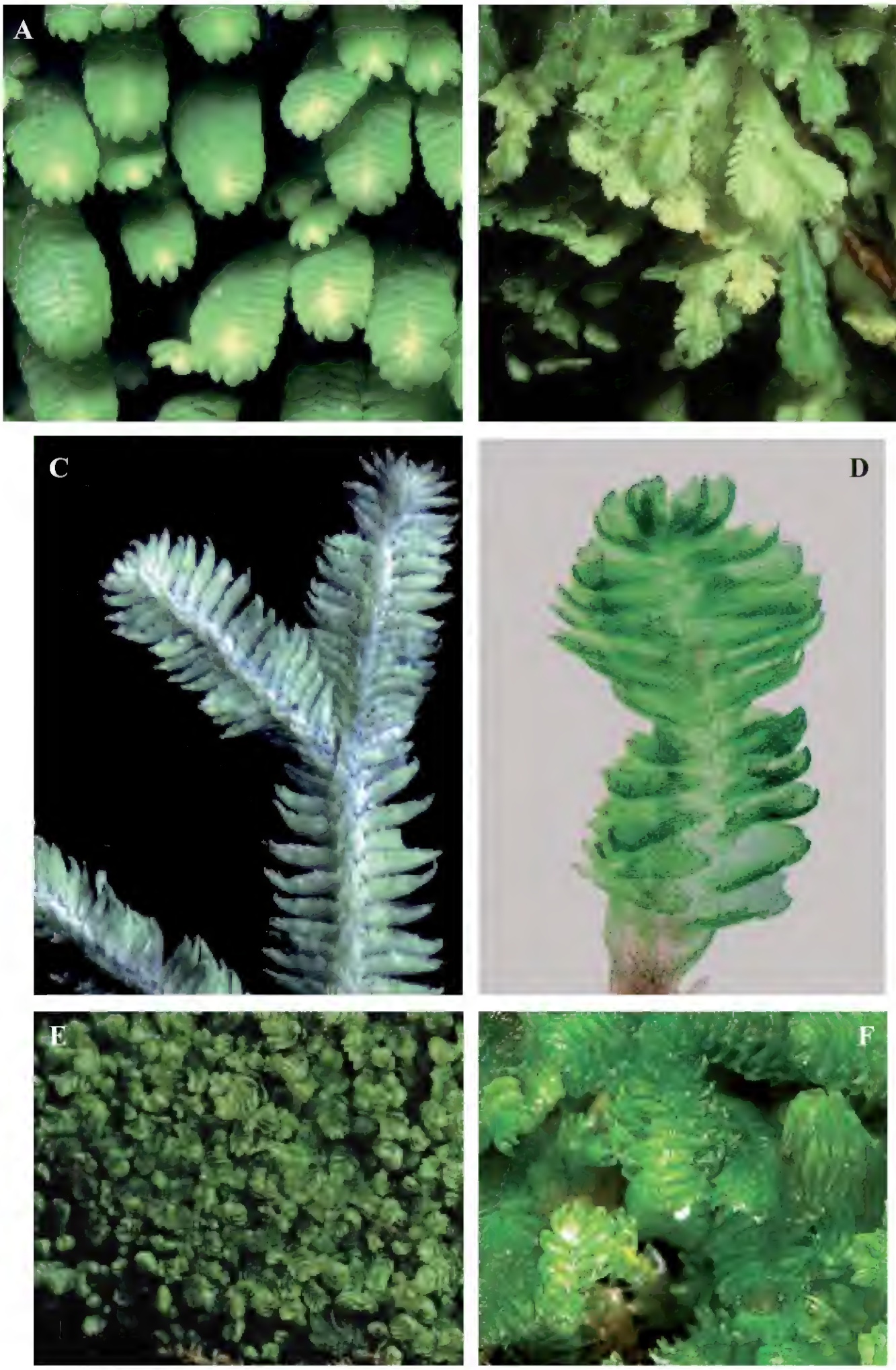


Plate 10

A *Lembidium nutans*, habit. Photo, W. Malcolm.

B *Lembidium longifolium*, habit. Photo, J. Braggins.

C *Lembidium longifolium*, single shoot, ventral view. Photo, W. Malcolm.

D *Chloranthelia berggrenii*, single shoot, dorsal view, showing notably fleshy stem. Photo, W. Malcolm.

E *Chloranthelia berggrenii*, habit. Photo, J. Braggins.

F *Chloranthelia berggrenii*, habit; note pure green color and fleshy stems. Photo, W. Malcolm.

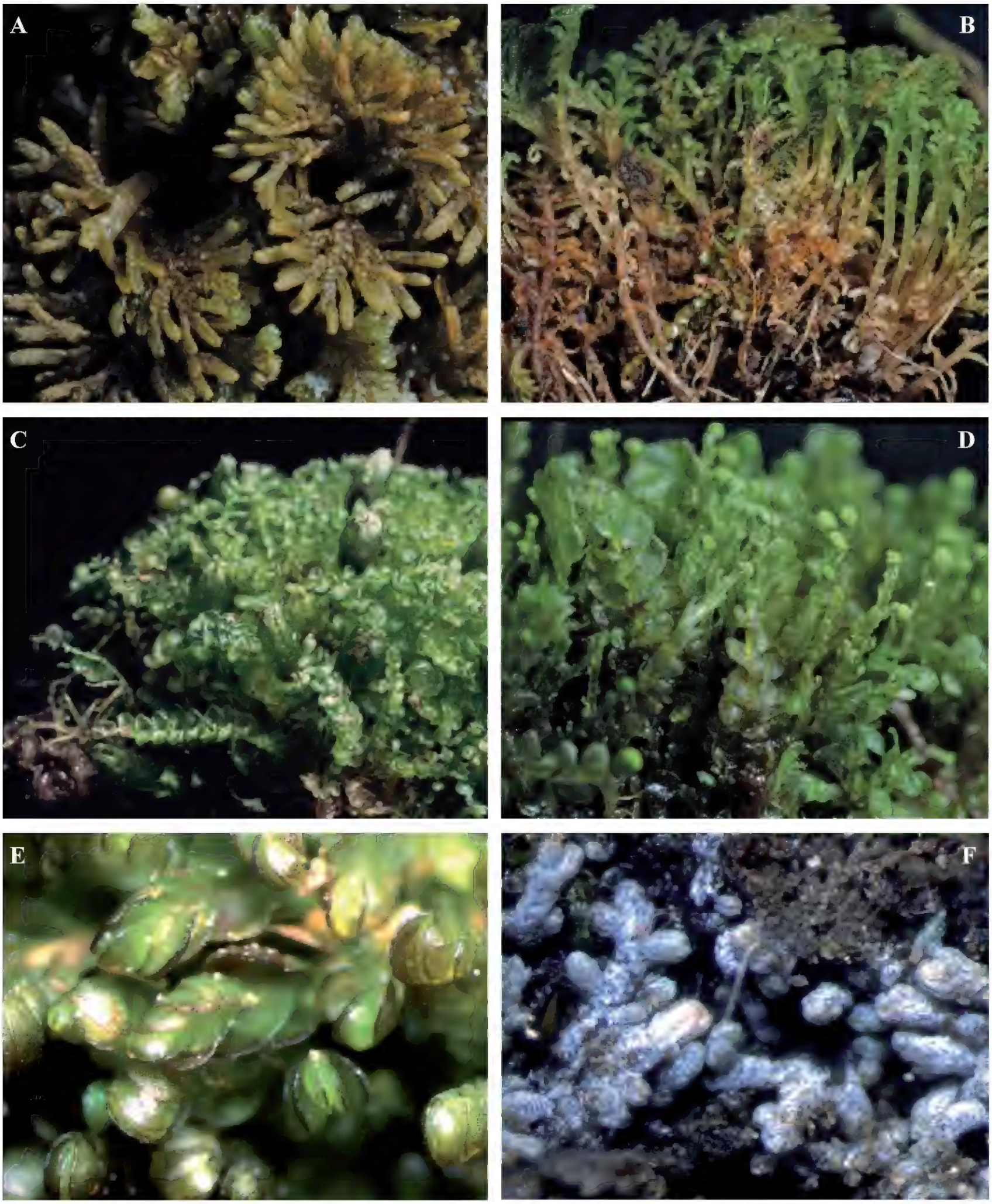


Plate 11

A *Megalembidium insulanum*, dendroid plants seen from above. Photo, J. Braggins.

B *Megalembidium insulanum*, erect shoots with pale spicate androecia toward bases. Photo, J. Braggins.

C *Hygrolembidum australe*, showing characteristic pure light green color, inflated perianths and deeply concave leaves. Photo, J. Braggins.

D *Calypogeia sphagnicola*, habit, showing attenuated gemmiparous shoot tips. Photo, J. Braggins.

E *Jackiella curvata*, habit. Photo, W. Malcolm.

F *Anthelia juratzkana*, habit; note whitish surface coating that covers all of plants. Photo, W. Malcolm.

Plate 12

A *Adelanthus gemmiparus*, distal sector of shoots. Photo, W. Malcolm.

B *Lophozia pumicicola*, habit, with perianths; note pigmentation. Photo, J. Braggins.

C *Pseudomarsupidium piliferum*, habit; note pair of awns at each of leaf apices. Photo, W. Malcolm.

D *Cuspidatula monodon*, shoot showing strongly dorsally assurgent leaves with protracted apices. Photo, W. Malcolm.

E *Adelanthus falcatus*, capsule and seta have emerged from shoot-calyptra with its attachment at the base of the plant. Photo, W. Malcolm.

F *Wettsteinia schusteriana*, shoot apex. Photo, W. Malcolm.

G *Allisoniella scottii*, whole plant showing perianth and ventral-intercalary branch at right. Photo, D. Glenny.

Plate 13

A *Solenostoma totipapillosum*, habit. Photo, W. Malcolm.
B *Solenostoma cryptogynum*, habit. Photo, W. Malcolm.
C *Anastrophyllum schismoides*, shoot apices, lateral view. Photo, W. Malcolm.
D *Solenostoma inundatum*, shoot apex showing transverse leaves. Photo, W. Malcolm.
E *Chandonanthus squarrosus*, habit. Photo, W. Malcolm.
F *Solenostoma hodgsoniae*, sterile shoots. Photo, J. Braggins.
G *Solenostoma hodgsoniae*; note yellowish antheridia in bract axils. Photo, J. Braggins.

Plate 14

A *Jamesoniella kirkii*, epiphytic and creeping over small hepatics. Photo, J. Braggins.

B *Jamesoniella colorata*, habit. Photo, J. Braggins.

C *Cryptochila pseudocclusa*, distal sector of shoot, lateral view; note tightly recurved leaf margins. Photo, W. Malcolm.

D *Cryptochila pseudocclusa*, single leaf showing recurved margin. Photo, W. Malcolm.

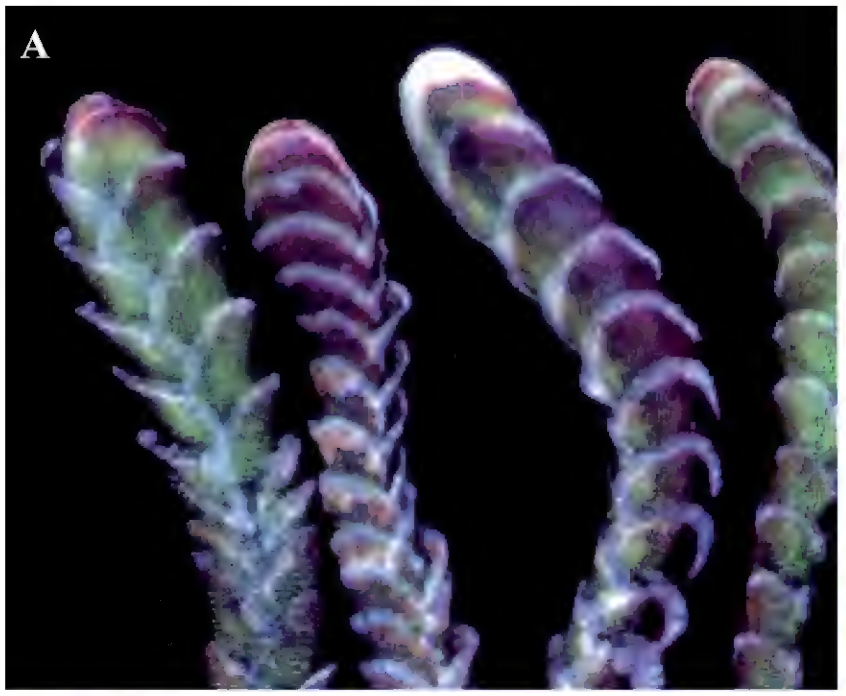
E *Cryptochila pseudocclusa*, gynoecium showing twisted perianth; note portion of incised-lobulate innermost bract visible at arrow. Photo, M. von Konrat & J. Engel.

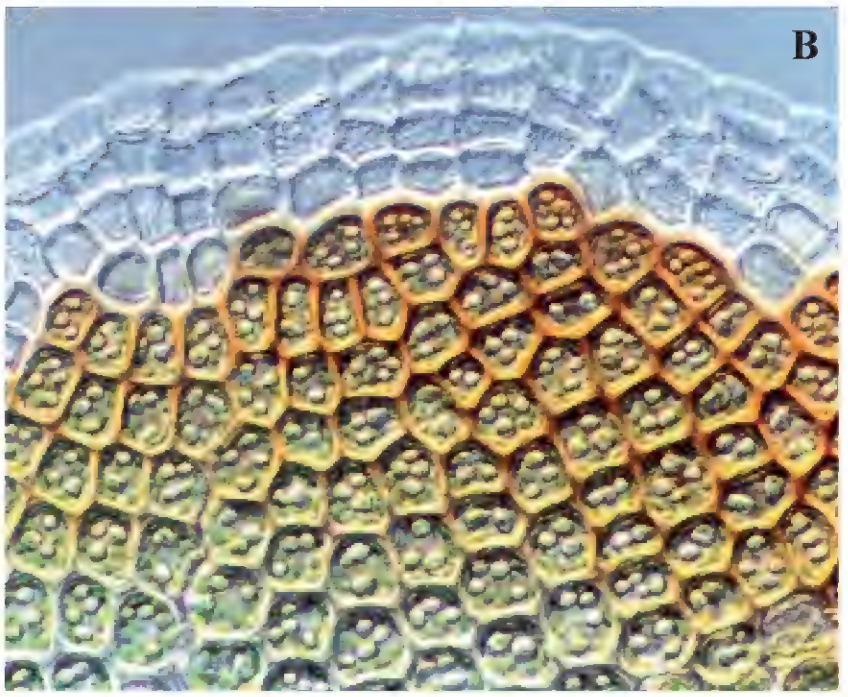
F *Jamesoniella tasmanica*, shoot apex, dorsal view. Photo, W. Malcolm.

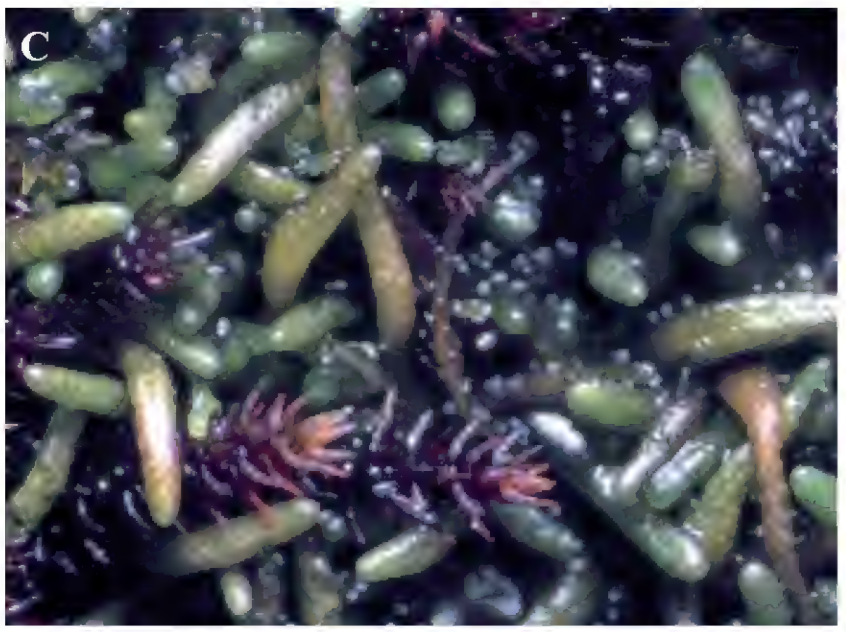
G *Jamesoniella colorata*, plant in moist state among mosses. Photo, W. Malcolm.

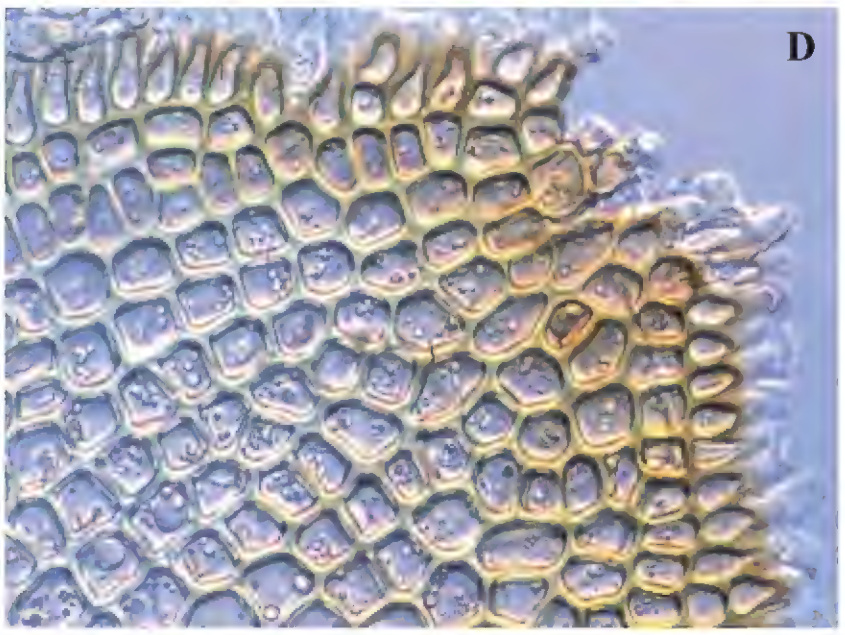
Plate 15

A *Diplophyllum domesticum*, perianth. Photo, W. Malcolm.
B *Scapania undulata*, distal sector of shoot, dorsal view. Photo, W. Malcolm.
C *Diplophyllum verrucosum*, shoots; note pigmentation. Photo, W. Malcolm.
D *Diplophyllum verrucosum*, distal sector of leaf. Photo, W. Malcolm.
E *Clandarium xiphophyllum*, shoots; note pigmentation. Photo, W. Malcolm.
F *Blepharidophyllum vertebrale*, shoots. Photo, W. Malcolm.









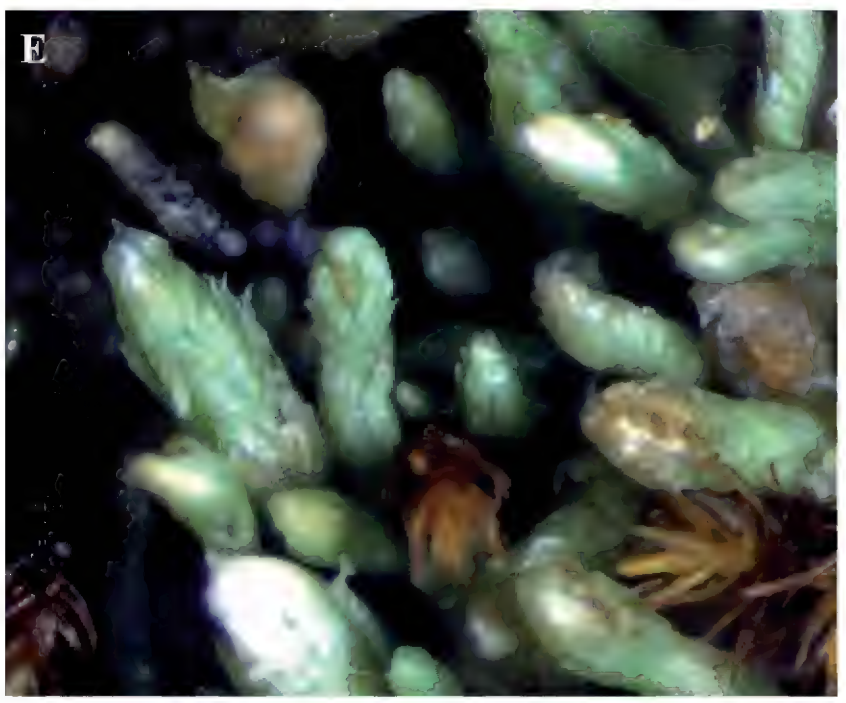


Plate 16

A *Herzogobryum teres*, distal sector of shoots. Photo, W. Malcolm.

B *Herzogobryum teres*, distal sector of leaf showing thin-walled hyaline margin and asperulate leaf surface. Photo, W. Malcolm.

C *Nothogymnomitrion erosum*, whole plants among *Andreaea.* Photo, W. Malcolm.

D *Nothogymnomitrion erosum*, leaf margins and apex, showing projecting marginal row of thick-walled cells. Photo, W. Malcolm.

E *Gymnomitrion cuspidatum*, whole plants. Photo, W. Malcolm.

F *Nothogymnomitrion erosum*, perianth and capsule. Photo, W. Malcolm.

Isotachis triloba Steph., Sp. Hepat. 3: 656. 1909. Type: New Zealand, South Is., Westland, Otira Gorge, *R. Brown* (G!).

Mastigophora beckettiana Steph., Sp. Hepat. 4: 35. 1909. Type: New Zealand, South Is., Canterbury, Waimate, May 1901, *Beckett 254* (G! – *c.* ♂, M!, CHR 585843 ex herb. Beckett!, MPN, hb. Hodgson no. 13200, *non vidi*).

Plants erect, olive-green, whitish green to pale brown to yellow-brown, the tips decurved, often magenta or orange-brown tinged, 15–30 mm long; shoots 1–3.4 mm wide. Branches rather common, of ventral- and lateral-intercalary types, often stoloniform, often with a system of prostrate stolons from which arise upright leafy shoots; *Frullania*-type branches rare. Stems with cortex in 1 layer, the exposed cell wall distinctly thickened, but the cells of ± similar size to those of the medulla; medullary cells thin. Leaves rigid, obscurely to distinctly ventrally secund, widely spreading (often at 90° angle with stem), 1.2–1.5(1.8)× longer than wide, the insertion recurved at dorsal end, the leaves concave, weakly to distinctly asymmetrically ovate to oblong-ovate to subrectangular, 2- or occasionally 3-lobed to 0.3–0.4, 0.4–1.4 mm wide × 0.6–2 mm long; lobes unequal, the dorsal larger, the third lobe (when present) the smallest, the lobes concave (often strongly so), mostly acute, sometimes apiculate, the tip terminating in a single cell or at most a uniseriate row of 3 cells, the lobe margins entire; lamina ca. 24–32 cells from dorsal sinus base to leaf base; dorsal margin dilated at the base, ± cordate; dorsal and ventral margins of lamina often with 1(2) processes at extreme base, the processes irregular, often laciniiform to lobuliform, often hook-like, the margins otherwise usually entire. Cells with walls evenly somewhat thickened, trigones distinct, mostly small to medium, occasionally large and bulging, median cells of lamina 17–30 μm wide, 25–38 μm long; surface densely striolate-papillose. Oil-bodies hyaline, 5–6 per cell, finely botryoidal, subglobose to narrowly to broadly elliptic. Underleaves slightly smaller than leaves, widely spreading, convex (ventral view), symmetrically ovate (often narrowly so) to oblong, 2- or occasionally 3-lobed to 0.25–0.3; lobes as in leaves; lamina margins each often with a process at extreme base similar to that of leaves, the margins otherwise entire, rarely with a tooth. Fungal partner absent.

Androecia on main shoot, terminal but eventually becoming intercalary; bracts more closely imbricate than leaves, in 4–6 pairs; bracts and bracteoles similar to leaves and underleaves except less deeply lobed, the lamina distinctly ventricose, the lamina margins often with a few coarse teeth; antheridia 2–3 per bract and bracteole, the stalk long (to 20 cells long). Gynoecia sporadic, on main shoot or leading branches; bracts of innermost series much larger than leaves, erect and ensheathing perianth, ventrally secund, asymmetrically ovate, 3-lobed, the dorsal lobe the largest, the lobes as in leaves; dorsal margin of lamina with a tooth or lacinia, the ventral with a few coarse teeth; bracteoles of innermost series similar to bracts in size and shape except the bracteoles are symmetrical and less deeply lobed, the lamina margins with a small tooth or entire. Perianth not demonstrably exserted beyond bracts, narrowly ovate, the base ± cylindrical, the distal half distinctly plicate, narrowing to the 9-lobed mouth, the lobes dentate below.

Capsule (*fide* Hässel and Solari, 1976) spherical, the wall 4–5 stratose, the outer wall with large nodules, the inner layer with large semiannular bands.

Spores 15 μm in diam., reddish brown, with small isolated papillae, or united and then with a vermiculate aspect. Elaters bispiral.

Distribution and Ecology: Amphi-Pacific temperate, occurring on Macquarie Island, New Zealand, Tasmania, the Philippines (Kitagawa, 1981), Tristan da Cunha, South Sandwich Islands, South Georgia, Falkland Islands, southern South America, southeastern Brazil, the

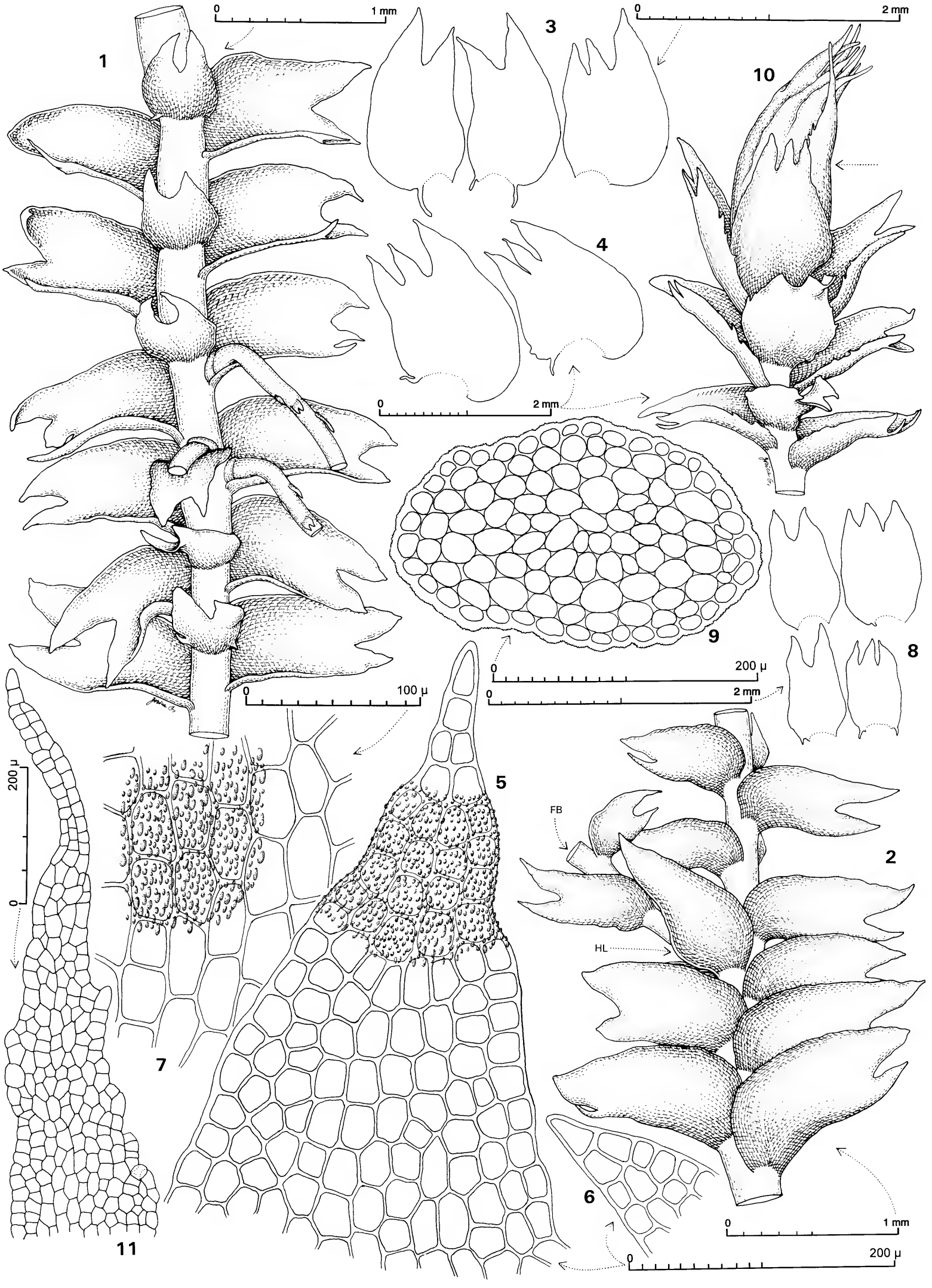


Fig. 16.
Triandrophyllum subtrifidum (Hook.f. & Taylor) Fulford & Hatcher. 1. Main shoot with 2 lateral-intercalary branches and 1 ventral-intercalary branch. 2. Portion of main shoot with *Frullania*-type branch (= FB; note half-leaf, = HL), dorsal view. 3, 4. Leaves. 5. Dorsal lobe of leaf (surface de-

Andes and Central America northward to Mexico. In New Zealand the species occurs on Campbell Island, Auckland Islands, Stewart Island, South Island (70–1520 m) and North Island (375–1400 m). Known in New Zealand from Fiordland Otago, Canterbury, Westland, Western Nelson, Marlborough, Sounds–Nelson, Southern North Island, Taranaki, Volcanic Plateau and Northland EPs. Less common in the North Island than South Island, and in the South Island not recorded much east of the Main Divide. The northernmost record is from Waipoua Forest.

A species of soil and rock, usually on stream banks or riverbanks, often within the flood zone where silt accumulates, but also on slips and overhanging banks of alluvial gravels. Recorded only once as an epiphyte, on Campbell Island. Found under lowland to upper montane forest and in open well-lit sites, and associated in such sites with *Breutelia pendula*, *Fissidens asplenioides*, *F. pungens*, *Isotachis lyallii*, *I. montana*, *Pyrrhobryum mnioides*, *Sematophyllum uncinatum* and *Symphyogyna undulata*. Also, on soil under overhanging banks with *Ditrichum difficile*, *Heteroscyphus triacanthus*, *Philonotis scabrifolia* and *Pohlia cruda*. Less commonly on stream banks and in rock crevices in the alpine zone up to 1580 m, and there found with *Andreaea subulata*, *Cryptochila grandiflora*, *Hepatostolonophora rotata* and *Herzogobryum teres*.

At stream-bank sites it can be the dominant species with little competition from other bryophytes, and its success in this habitat seems to be due to its tolerance to periodic inundation by fast-flowing water and its ability to grow out of the sediment that becomes trapped among the shoots.

Comments: The species is divided by Solari (1973) into three varieties. Variety *subtrifidum* is amphi-Pacific, var. *trifidum* (Gottsche) Solari is Andean American in distribution and var. *fuscum* (Steph.) Solari occurs only in southern South America. Only the typical variety occurs in New Zealand. Hodgson (1967) cites specimens of *T. trifidum* from eastern and central North Island, distinguished from *T. subtrifidum* by lower leaf and underleaf margins with numerous teeth. Hodgson found no other character distinguishing the two species but followed Fulford and Hatcher (1961) to arrive at these identifications.

The taxon is most similar to *Herbertus oldfieldianus* and the two *Lepicolea* species, with which it shares deeply bifid to 4-fid leaves and a vitta, but is usually found in quite a different habitat. Also, the plants are erect rather than pendent, shorter and not hoary. Its leaves are more patent to the stem than in those two genera, and are less densely imbricate on the stem.

Fulford (1963b) and Fulford and Hatcher (1959) state that only two kinds of branches are found in the genus: ventral-intercalary and, rarely, lateral-terminal, *Frullania*-type branches. Branching in *Triandrophyllum* is of the ventral- and lateral-intercalary types (Fig. 16: 1), both rather common, but terminal, *Frullania*-type branches are rare. They apparently occur only in *T. subtrifidum* (Fig. 16: 2).

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tail shown in part). 6. Distal portion of dorsal lobe of leaf. 7. Median leaf cells (surface detail shown in part). 8. Underleaves. 9. Stem, cross section. 10. Mature gynoecium (old sporophyte not shown), ventral view, the arrow indicates maximum depth of sinus on ventral-lateral side. 11. Lobe of perianth mouth. (Figs. 1–3, 5–9, from *Engel 17756*, New Zealand, South Is., Otago EP, Mt. Maungatua; 4, from *Engel 21064*, New Zealand, North Is., Northland EP, Waipoua R.; 10–11, from *Hatcher 654*, New Zealand, South Is., Fiordland EP, trail between Gunns Camp and Hidden Falls.)

Type plants of *Mastigophora beckettiana* represent a short, caespitose form of *T. subtrifidum*. These differ from normal ♂ plants only in the slightly smaller size, owing to the habitat (as the label states) "on hills, among grass"—in a relatively xeric site.

Family **PSEUDOLEPICOLEACEAE** Fulford & J.Taylor

Pseudolepicoleaceae Fulford & J.Taylor, Nova Hedwigia 1: 411. 1960.
Blepharostomataceae Müll.Frib., Svensk Bot. Tidskr. 42(1): 14. 1948, *nom. inval.*; R.M.Schust., Amer. Midl. Nat. 49: 302. 1953, *nom. inval.*; Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland, ed. 3. 6: 590. 1954, *nom. inval.*; S.W.Arnell, Illus. Moss Fl. Fennoscandia 1: 47. 1956, *nom. inval.*
Herzogiariaceae Fulford, Nova Hedwigia 1: 397. 1960.
Chaetocoleaceae Fulford, Mem. New York Bot. Gard. 11: 62. 1963.

Plants isophyllous to moderately anisophyllous, erect to procumbent, green to brown to fuscous, but reddish pigmentation lacking; plants small to robust. Branching sparing, irregular, commonly of *Frullania* and ventral-intercalary types, rarely of *Microlepidozia*, *Acromastigum*, or lateral-intercalary types. Stems with surface lacking paraphyllia, in cross section with cortex typically poorly differentiated, of thin-walled or moderately thick-walled cells ± similar to the medullary cells or a little smaller. Rhizoids often only sparingly developed, from stem at underleaf bases or from cells of underleaf. Leaves with insertion transverse to succubous (at times weakly incubous in *Isophyllaria*), often stiffly spreading from stem, not ventrally secund, symmetric to rather asymmetric (and with dorsal lobe[s] smaller), typically quadrifid (at times bisbifid, sporadically 3-lobed, bifid in *Isophyllaria*), often with marginal teeth or cilia, at least in the vicinity of gynoecia. Cells normally ± rectangular and moderately to distinctly longer than wide, often ± in tiers, not forming a vitta, typically thin- or firm-walled and lacking trigones (except *Archeophylla*, where trigones are nodulose); surface usually striate-papillose. Oil-bodies finely granular to papillose. Underleaves similar to leaves but always symmetrical. Asexual reproduction lacking (except *Blepharostoma*, with 1-celled gemmae from leaf lobe tips and *Chaetocolea*, with fragmentation of teeth and lobes of leaves).

Dioecious (except in some species of *Blepharostoma* and *Lophochaete*). Androecia on leading leafy shoots, rarely on ± abbreviated lateral branches, becoming intercalary; bracts often leaf-like but somewhat to strongly pouched at base and commonly less deeply lobed, usually with 1–2 antheridia; antheridial stalk 2-seriate (uniseriate in *Blepharostoma*); bracteoles without antheridia. Gynoecia on leading leafy shoots; bracts and bracteoles like the leaves and underleaves but typically larger and less deeply lobed. Perianth present, 3–6-plicate, the mouth wide (contracted in *Archeophylla*); perianth distinct and well developed, the mouth ciliate or dentate; coelocaule-precursor lacking (*Archeophylla*) or present; calyptra well developed but a shoot-calyptra at times somewhat elaborated.

Seta of numerous cells, with 12–20 rows of outer cells surrounding an internal core of cells ± similar in size (8+4 rows in *Blepharostoma*). Capsule ovoid or ellipsoidal, the wall 3–5-layered (2-layered in *Blepharostoma* and *Lophochaete*); epidermal cells with or (some *Temnoma*) without radial (nodular) thickenings; inner cells with conspicuous radial (nodular) or semiannular bands. Spores small, 1–2× the elaters in diam., finely granular or papillose or vermiculate.

Type: *Pseudolepicolea* Fulford & J.Taylor

We are circumscribing the *Pseudolepicoleaceae* to include three subfamilies. Subfamily *Blepharostomatoideae* Grolle has one genus, *Blepharostoma* (Dumort.) Dumort., a basically Holoarctic genus with three species. One species, *B. trichophyllum* (L.) Dumort., is circum north-temperate–subarctic–Arctic, but extends southward in three major areas: to Java and New Guinea; to montane–alpine regions of Africa (the only member of the family to occur in Africa); and to Central America and the Andes. Subfamily *Chaetocoleoideae* R.M.Schust., with the monotypic genus *Chaetocolea* Spruce, occurs at high elevations in the northern Andes.

Subfamily *Temnomoideae* R.M.Schust. has seven genera and all but one of these are southern temperate–subantarctic. The exception is *Lophochaete* R.M.Schust., with three species, which is Laurasian–Himalayan in range (for included species see Schuster, 1966b). Of the seven southern temperate–subantarctic genera, three (*Archeophylla*, *Isophyllaria* and *Temnoma*) are treated here and the following three are outside of our area. *Archaeochaete* R.M.Schust. has three species, one (*A. kuehnemannii* R.M.Schust.) from southern South America and the Falkland Islands (see Schuster, 1966b; Engel, 1978, 1990a), one from Tristan da Cunha (*A. temnomoides* R.M.Schust.), and one from alpine New Guinea (*A. grolleana* R.M.Schust.). *Archeochaete* is sometimes included in *Pseudolepicolea* (e.g., Hässel, 1974; Grolle, 1983). *Herzogiaria* Fulford, with only *H. teres* (Steph.) Fulford of southern South America (see Hässel and Solari, 1976; Hässel, 1981). *Pseudolepicolea* Fulford & J.Taylor, with one species, *P. quadrilaciniata* (Sullivan) Fulford & J.Taylor, of southern South America and South Georgia (see Hässel and Solari, 1976; Schuster, 2000a).

A fourth subfamily (subfam. *Trichocoleoideae*) is sometimes included here (Schuster, 1980c, 1984e, 2000a, 2001d). This strongly tropical group is here treated at the rank of family (*Trichocoleaceae*).

Isophyllaria E.A.Hodgs. & Allison

Isophyllaria E.A.Hodgs. & Allison *in* E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 68. 1965.
Fulfordiella Hässel, Comun. Mus. Argent. Ci. Nat. "Bernardino Rivadavia," Bot. 2: 48. 1974.

Plants isophyllous (especially distally), rigid, fuscous to nearly black, rather small, 7–12 mm long, 0.5–1 mm wide with leaves. Branching irregular, sparing to rather frequent, mostly ventral-intercalary and leafy or stoloniform and whip-like, the stoloniform branches variable in position, in median as well as lower sectors of shoot; *Frullania*-type branches at times frequent; lateral-intercalary branches rare. Stem wiry, the cortex in surface view striolate, in cross section in 1 layer of ca. 20 rows of thick-walled cells larger than those of the medulla; medullary cell walls thin, thickened in the corners. Rhizoids from stem at underleaf bases, the tips branched. Leaves rigid, spreading, loosely imbricate, closely imbricate near shoot apices, unistratose, dorsally assurgent, the disc stiffly and widely spreading but the lobes incurved and forming a broad arch, the insertion transverse to weakly succubous, the leaves cuneiform, the base narrow, the leaves ± symmetric, bifid to 0.5–0.7, 400–450 μm wide × 650–1100 μm long; lobes subequal, divergent, often ± twisted, plane or weakly abaxially canaliculate (except at apices), tapered, lanceolate-acuminate, terminating in 1(2) cells or (ours) a uniseriate row of 2–4 ± isodiametric cells, the lobe margins entire; sinus ± rounded at base, the margin reflexed; disc obcuneate, entire. Cells evenly and distinctly thick-walled, the distal and marginal cells of lobes + marginal cells of disc ± isodiametric, the intramarginal cells wider and longer and forming a subvitta that extends into the lobe bases (the cells of the subvitta at most 2:1); median cells of disc 13–18 μm wide × 24–35 μm long; surface of

lobes striate-papillose, of disc conspicuously long-striate. Oil-bodies dull and opaque, faintly greyish, 2–4 per median cell of lamina, obscurely and faintly coarsely granular, mostly globose and 2.5–4 μm in diam., less often broadly elliptic and 2.9 × 3.8–4.6 μm. Underleaves transversely inserted, similar in size and form to leaves or a little smaller. Asexual reproduction absent.

Dioecious. Androecia on long leafy shoots, becoming intercalary, the bracts in 2–7 pairs, subequal to leaves in size and basic form, contiguous to feebly imbricate, the disc sharply ventricose; antheridia 1–2 per bract, the stalk biseriate; bracteoles appressed to stem, smaller than bracts. Gynoecia with bracts and bracteoles similar in form to leaves and underleaves but larger, the lobes often twisted, with recurved margins, shallowly sulcate, the margins entire; coelocaule-precursor present, short, the bracts and bracteoles of 2 series becoming elevated on the coelocaule-precursor and inserted on it. Perianth exserted, linear-elliptic in outline, bluntly trigonous in distal half or a little more, weakly narrowed to the rather wide and open, at times slightly contracted mouth; mouth shortly dentate, the teeth comprised of a few cells.

Seta with an outer row of 16 cells surrounding an inner core of 9 or (*Isophyllaria fuegiana*) 17 somewhat smaller cells. Capsule spherical to short-cylindrical, in 3–4 layers; outer layer of cells with red or vinaceous nodular thickenings on longitudinal and transverse walls; innermost layer of cells with red or vinaceous nodular or sinuous-nodular thickenings, semiannular bands lacking.

Spores 12.5–16 μm in diam., red or red-brown, with vermiculate markings that often anastomose and some papillae (*Isophyllaria attenuata*), or densely granulate (*I. fuegiana*).

Elaters tortuous, bispiral throughout or bispiral in median sector and unispiral at the ends.

Type: *Isophyllaria murrayana* E.A.Hodgs. & Allison

A genus with two closely related species, *Isophyllaria attenuata* and *I. fuegiana* (Hässel) R.M.Schust. of southern South America. Hässel (1974) described *Fulfordiella fuegiana* Hässel (type: Chile, Tierra del Fuego, Río Azopardo, 600 m, *leg. Dusén*), but later (Hässel, 1981) placed the species in the synonymy of *I. attenuata*, a plant described from Tasmania. Schuster (2000a) transferred *F. fuegiana* to *Isophyllaria*, and differentiated the Australasian populations by the transverse to weakly succubous leaves with lobes narrowly lanceolate and terminating in a uniseriate row of 2–4 cells vs. the transverse to weakly incubous leaf insertion and the narrowly or shortly acute leaf lobes that end in 1(2) cells in the southern South American *I. fuegiana*. Schuster (2000a) also differentiated the two species on branching: presence of *Frullania*-type branching in *I. fuegiana* vs. their absence in *I. attenuata*. However, terminal branches in the latter species are present and rather common, though less abundant than those of the ventral-intercalary type. Other characters found in *I. fuegiana* require further evaluation as they relate to *I. attenuata*. For example, *I. attenuata* has microphyllous shoots below ground (Hässel, 1981) vs. a more general distribution in the median as well as lower sectors of shoots in *I. fuegiana*.

References: Hodgson (1965); Hässel (1974, 1981); Schuster (1966a, 2000a).

Isophyllaria attenuata (Rodway) E.A.Hodgs.

[Figs. 17–19]

Isotachis attenuatus Rodway, Tasman. Bryoph. 2: 62. 1916. *Isophyllaria attenuata* (Rodway) E.A.Hodgs., J. Roy. Soc. New Zealand 2: 111. 1972. Type: Tasmania, Mt. Wellington Plateau.
Isophyllaria murrayana E.A.Hodgs. & Allison *in* E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 68. 1965. Holotype: New Zealand, Stewart Is., Mt. Allen, Feb. 1949, *Murray 2193* (MPN ex herb. Hodgson 11720).

Plants with branches mostly ventral-intercalary; *Frullania*-type branches rather common but less abundant than intercalary branches. Leaves 320–400 μm wide × 620–760 μm long, bifid to 0.65–0.75; lobes narrowly lanceolate, plane or weakly abaxially sulcate (except at apices), terminating in a uniseriate row of 2–4 subisodiametric cells, often with a number of biseriate tiers basal to the uniseriate row, the ultimate row of cells of the lobes + the cells of uniseriate row each with a biconvex thickening of the exposed wall (depending on the plane of focus but seen at least in profile), the inner portion of the lenticular thickening often occupying a distinct volume of the cell lumen, the uniseriate portion often submoniliform; disc marginal cells with sublenticular thickenings as in lobes. Cells of leaf with middle lamella distinct, the cells in median sector of disc 13–16 μm wide × 22–35 μm long. Oil-bodies occurring throughout leaf, occupying a small portion of cell lumen, dull and opaque, faintly greyish, 2–4 per median cell of lamina, the number the same throughout leaf, obscurely and faintly coarsely granular, appearing roughened, the granules slightly protruding beyond the membrane, the oil-bodies mostly globose and 2.5–4 μm in diam., less often broadly elliptic and 2.9 × 3.8–4.6 μm. Chloroplasts large for cell size.

Gynoecia with bracts and bracteoles gradually grading in size to vegetative leaves, those of innermost series similar in form to leaves and underleaves but larger and distinctly concave, cuneiform from a narrow base, the lobes often twisted, with recurved margins, shallowly sulcate, the lobe and lamina margins entire. Perianth at most 0.35 exserted, at times barely exserted beyond bracts, ovate to short-elliptic in outline, bluntly trigonous in distal half or a little more, shallowly plicate distally, weakly narrowed to the rather wide and open, at times slightly contracted mouth; mouth irregularly dentate, the teeth small, thick-walled and with a striate-papillose surface, often consisting merely of a uniseriate row of 2 cells or a biseriate tier + a single cell, occasionally with 2 biseriate tiers + a uniseriate row of 2 cells, the terminal cell at most slightly longer than wide, tapered to a rounded summit.

Seta with an outer row of 16 cells surrounding an inner core of 9 somewhat smaller cells with straight to bulging corner thickenings. Capsule spherical, the walls fragile and easily fragmenting, in 3 layers, 30–35 μm thick; outer layer thicker than inner layers combined, the outer layer of cells subquadrate to short- (both transversely and longitudinally) rectangular, walls moderately thickened, the longitudinal and transverse walls with vinaceous nodular thickenings; innermost layer of cells variable in shape and short- to long-subrectangular, the walls ivory-white and moderately to markedly thickened, with vinaceous sinuous-nodular thickenings, a thin, sheet-like, vinaceous-pigmented thickening often also present on the radial between the nodular thickenings, semiannular bands lacking.

Spores 12.5–14.4 μm in diam., red-brown, with low but sharply defined, dense, vermiculate markings that often anastomose + some papillae. Elaters tortuous (often merely C-shaped), 6.7–8.2 μm wide, gradually tapered toward the tips, bispiral throughout or bispiral in median sector and unispiral at the ends, the spirals 2.9–3.8 μm wide.

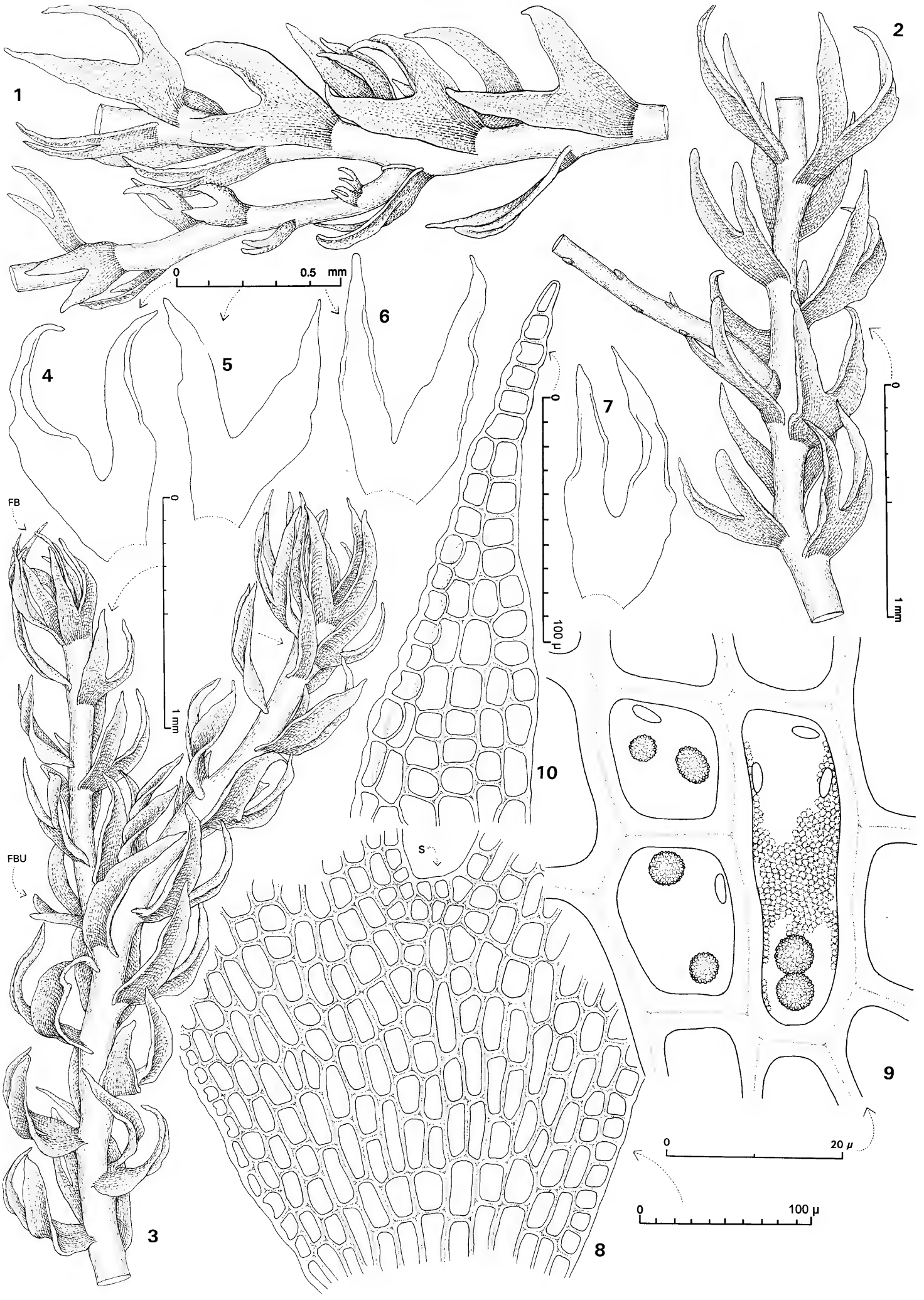

Fig. 17.
Isophyllaria attenuata (Rodway) E.A.Hodgs. 1, 2. Portions of leading shoots (ventral-lateral views and drawn to same scale), each with a ventral-intercalary branch, at left with a leafy branch, at right with a stoloniform branch; note the dorsally assurgent leaves. 3. Portion of shoot with *Frullania*-type branch (= FB), dorsal view; note half-leaf and 3-lobed first branch underleaf (= FBU); note also accessory lobe toward apex of main shoot (at arrow). 4–7. Leaves (abaxial aspect), all drawn

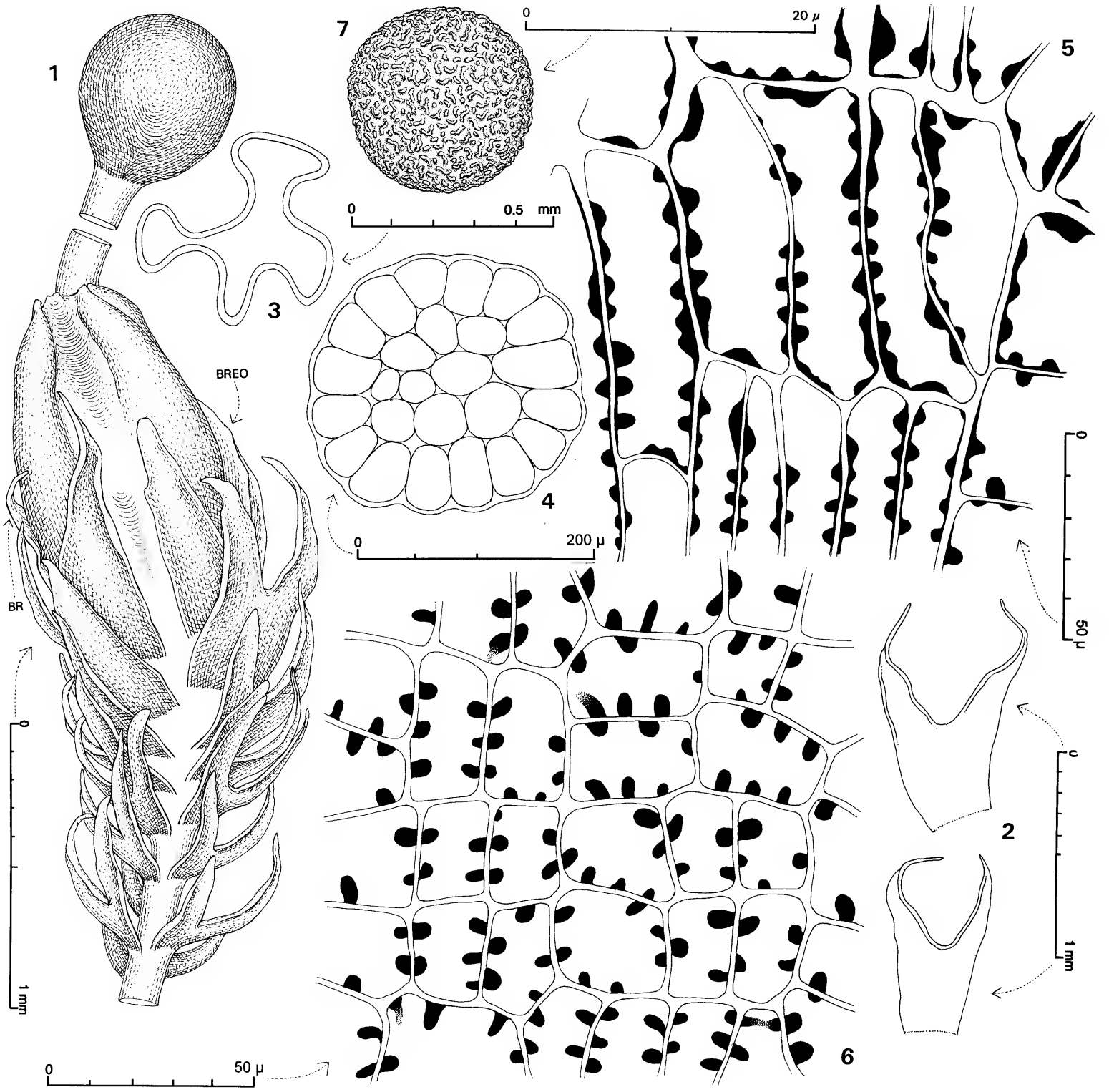

Fig. 18.
Isophyllaria attenuata (Rodway) E.A.Hodgs. 1. Gynoecium with mature sporophyte, ventral-lateral view (BR = bract; BREO = bracteole); note gradual transition from vegetative leaves and underleaves to bracts and bracteoles. 2. ♀ Bract, and lower, bracteole (abaxial aspect). 3. Cross section through distal third of perianth. 4. Seta, cross section. 5. Capsule wall, outer layer. 6. Capsule wall, inner layer. 7. Spore. (All from *Glenny 9201*, New Zealand, South Is., Westland EP, Upper Otira Valley.)

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to same scale. 8. Portion of leaf lamina and lobe base showing subvittate condition; note ± isodiametric cells at leaf margins and (at left) ± lenticular thickenings of exposed wall (S = sinus base). 9. Median leaf cells with oil-bodies. 10. Distal portion of leaf lobe; note that lenticular thickenings may be seen when margin is viewed in ± profile. (Figs. 1–8, 10, from *Engel 22004*, New Zealand, South Is., Fiordland EP, head of Gertrude Valley; 9, from *Glenny 9201*, New Zealand, South Is., Westland EP, Upper Otira Valley.)

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, Stewart Island (750–960 m), South Island (1050–1970 m), North Island (520–1700 m); Australia: Tasmania. In New Zealand known from Rakiura (Mt. Allen, Mt. Anglem), Fiordland (Mt. Burns, Eldrig Peak, Lake Wapiti, Gertrude Valley), Westland (Upper Otira valley), Western Nelson (Mt. Euclid) and Volcanic Plateau (Mt. Ruapehu, Waimiha Stream) EPs.

The species usually occurs in the alpine zone where it may be found on moist or at times irrigated exposed rock and in snow-melt stream courses, granite and greywacke in the South Island and Stewart Island, or volcanic rock on Auckland and Campbell islands and Mt. Ruapehu. For example, it occurs at 1940–1970 m in seepage over rock domes at the head of Gertrude Valley, Fiordland Natl. Park. Invariably it has been found accompanied by *Hepatostolonophora rotata* var. *perssonii*, but is also found with *Allisoniella scottii*, *Blindia robusta*, *Cephalomitrion aterrimum*, *Cryptochila acinacifolia*, *Isotachis intortifolia*, *Pachyglossa tenacifolia*, *Rhacocarpus purpurascens*, *Riccardia aequicellularis* and *R. aequitexta*.

Comments: The species should not confused with a ny other except perhaps small, deeply pigmented phases of *Herbertus*, a plant that, like *Isophyllaria*, is isophyllous with both leaves and underleaves deeply bifid, and that has frequent ventral-intercalary branching. Plants of the

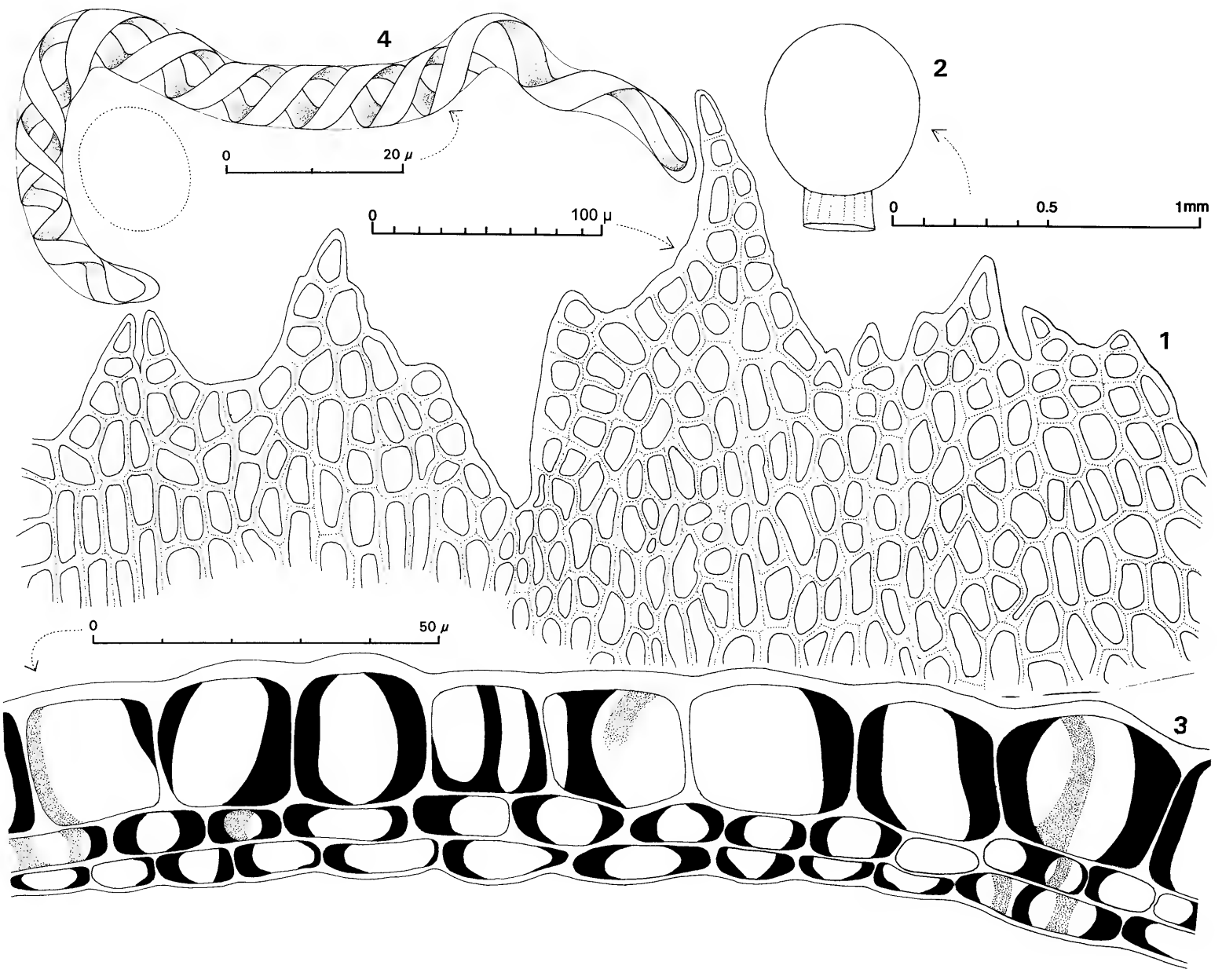

Fig. 19.
Isophyllaria attenuata (Rodway) E.A.Hodgs. 1. Portion of perianth mouth. 2. Capsule profile. 3. Capsule wall, cross section. 4. Elater and spore outline drawn to same scale. (All from *Glenny 9201*, New Zealand, South Is., Westland EP, Upper Otira Valley.)

much smaller *Isophyllaria*, however, may be differentiated by the leaves being less imbricate on the stem, the evenly and markedly thick-walled cells, the weakly defined vitta and the symmetric, dorsally assurgent, stiffly spreading leaves with incurved, arched lobes vs. the presence of massive trigones separated by narrow, thin-walled places, the sharply defined vitta and the asymmetric, ventrally secund leaves in *Herbertus*.

Temnoma Mitt.

Temnoma Mitt. *in* Hook.f., Handb. N. Zeal. Fl. 753. 1867. *Teinnoma* Mitt., Philos. Trans. 168 (extra vol.): 32, 33. 1879, *err. typogr.*

Plants isophyllous to weakly anisophyllous, suberect to procumbent, deep green to commonly brown, small to medium in size, 0.8–3.5 mm wide with leaves. Branching rather sparing, irregularly variable: *Frullania* type always present, ventral-intercalary type typically present but at times infrequent; *Microlepidozia* and *Acromastigum* types rarely present in some taxa; lateral-intercalary very rare (*T. quadrifidum*). Stems with cortical cells ± thin-walled, ± equal in size to the thin-walled medullary cells or a little smaller. Rhizoids at underleaf bases. Leaves with insertion nearly transverse to weakly to distinctly succubous, symmetric or, less often, asymmetric (the dorsal 1–2 lobes smaller), (3)4-lobed to (0.2)0.25–0.75; lobes acute to lanceolate, entire or with opposed, spinescent, normally unbranched teeth or cilia (at least near sinuses, or near gynoecia); disc entire or with teeth or cilia. Cells of lamina rectangular, typically conspicuously so, for the most part 1.5–3× longer than wide, thin- to weakly firm-walled, without trigones, the areolation irregular and not in a tiered arrangement; surface typically conspicuously striate-papillose. Oil-bodies granular to finely papillose. Underleaves 2(4)-lobed, entire or with teeth or cilia similar to those of the leaves. Asexual reproduction absent.

Dioecious. Androecia on long leafy shoots, becoming intercalary, the bracts similar to leaves except moderately to distinctly ventricose at base and less deeply lobed; antheridia 1–2 per bract, the stalk biseriate; bracteoles flat. Gynoecia with bracts and bracteoles erect and sheathing perianth, like the leaves and underleaves except larger and the disc higher, the lobes dentate to ciliate (even if leaves and underleaves entire or subentire), the teeth larger than those of leaves and underleaves; coelocaule-precursor present, distinct, the bracts and bracteoles + 1 or more gyres of leaves and underleaves becoming elevated on the coelocaule-precursor and inserted on it. Perianth arising from the coelocaule-precursor, trigonous above, not or at most moderately narrowing to the wide and open, distinctly dentate to ciliate mouth, the armature at times setose.

Seta with 10–20 outer cells surrounding 16–32 internal cells (Schuster, 2000a). Capsule ovoid-ellipsoidal, the wall 3–5-layered; outer layer of cells markedly large, hyaline, with weak or small nodular thickenings or with thickenings absent (except along the valve margins); innermost layer of cells with semiannular bands, the bands complete or incomplete.

Spores punctate or minutely vermiculate or weakly verruculose, 1–2× the elaters in diam. Elaters tortuous, short, bispiral, the spirals narrow.

Type: *Temnoma pulchellum* (Hook.) Mitt. (≡ *Jungermannia pulchella* Hook.)

All but two of the *Temnoma* species are southern temperate–subantarctic in range; the exceptions are *T. chaetophyllum* R.M.Schust., a species occurring at high elevations of Venezuela and Colombia (Schuster, 1978; Gradstein et al., 2001), and *T. setigerum* (Lindenb.)

R.M.Schust., of New Caledonia, New Guinea, Fiji, Solomon Islands, Java, Philippines to Taiwan, Hawaii (Schuster, 1966a, 2000a; Piippo, 1984).

Two species occur in southern South America, *Temnoma pilosum* (A.Evans) R.M.Schust. and *T. quadripartitum* (Hook.) Mitt., an amphi-Pacific temperate species that is also present in New Zealand (see Schuster, 1967a; Hässel and Solari, 1976; Engel, 1978). Hässel and Solari (1976) recognized a third species, *T. subintegrum* Fulford, which was placed in the synonymy of *T. quadripartitum* var. *randii* (S.W.Arnell) R.M.Schust. by Schuster (1966a) and Engel (1978).

Six of the 11 known species occur in New Zealand and most are endemic there.

References: Hodgson and Allison (1962; rev.); Schuster (1967a, rev.; 2000a).

The following key and treatment of taxa are adapted, with considerable modification, from Schuster (1967a).

Key to Species

1a. Leaf lobes narrow, ± gradually tapered into the uniseriate distal portions (or lobes uniseriate to base); cells of uniseriate row (if any) usually striolate like laminar cells, not normally exceeding 3–5× longer than wide (under 85[95] μm long); branching variable: with some *Frullania*-type branching, but usually some or many branches ventral-intercalary, rarely lateral-intercalary, with *Microlepidozia*- or *Acromastigum*-type branches occasional; leaf insertion nearly or quite transverse, the orientation subtransverse; underleaves (0.5)0.6–0.9(1)× the leaves in area 2

2a. Mature leaves of sterile shoots with cilia (or teeth), if present at all, usually lying in plane of leaf; leaves 0.4–0.65(0.75) quadrifid, the disc usually (5)6–9 or more cells high; lobes of ♀ bracts (and subfloral leaves) each with 1–2 to 3–5 pairs of stiff teeth or cilia, the lobe apices formed of cells up to 2–4(6)× longer than wide. Juvenile (and sometimes mature) leaves often lacking cilia or marginal teeth, each leaf lobe with at most 1–2(3) pairs of cilia or teeth, each formed of 1–3(4) cells 3

3a. Leaves (and some underleaves) in large part appearing palmately 5–6-lobed, tending to produce a large, lobe-like tooth at one or both disc bases, the margins otherwise ± edentate, the lobes usually entire; leaves squarrose. Leaf lobes usually (2)3–6(11) cells broad at base, acuminate, ending in tips of (2)4–6(8) subisodiametric or slightly elongated cells; disc 5–8 cells high . . . . . *T. quadripartitum* (p. 158)

3b. Leaves (3)4-lobed, never with large, lobe-like teeth or appendages of leaf bases (cilia of disc margins, if present, suprabasal and never lobe-like); leaves suberect to obliquely or widely patent, never squarrose 4

4a. Leaves with disc margins edentate (except occasionally below gynoecia); leaves frequently bisbifid, with median sinus clearly deeper; leaf lobes blunt to acute but not acuminate, normally ending in a single cell or 2–4(5) superposed cells that are only slightly elongated (1–2.5:1); underleaves usually almost identical in size to lateral leaves; branches mostly ventral-intercalary . . . . . *T. quadrifidum* (p. 156)

4b. Leaves with disc margins commonly bearing 1–4 slender, sharp, suprabasal cilia or teeth; leaves not bisbifid, the sinuses equal; leaf lobes acuminate, ending in cilia of 3–5 to 7–8 superposed cells that are, in part, elongated (ca. 2.5–5:1); underleaves clearly smaller than lateral leaves; branches of *Frullania* and ventral-intercalary types . . . . . *T. palmatum* (p. 161)

2b. Mature leaves of sterile and ♂ shoots (not gynoecial plants alone) at least in large part with cilia or teeth well developed at and near sinus bases and along margins of disc, the lower teeth of disc margins occasionally reflexed (occasionally enlarged to simulate accessory lobes), the cilia or teeth near sinus bases sharply reflexed or displaced, abaxially projecting, not lying in leaf plane; leaves usually (0.65)0.7–0.85 quadrifid (rarely trifid), the disc (2)3–5 cells high to (large forms) 5–6(8) cells high; lobes of ♀ bracts with numerous (to 7–8 pairs) cilia or spines, the lobe apices formed of cilia or setae 350 μm long or more (5–6 superposed cells or longer). Teeth of leaf lobes short, rigid, spine-like, abruptly tapering, not ciliiform, of (1)2–4(5) superposed cells, the cells subisodiametric; lobes (3)4–5 to 5–6(8) cells wide at base . . . . . *T. quadripartitum* (p. 158)

1b. Leaf lobes ± broadly acute at base, each abruptly narrowed into a highly differentiated, elongated, setose uniseriate distal portion; cells of uniseriate row usually smooth, strongly elongated (to 100–135 μm long); branching not variable: either all or most branches of the *Frullania* type, or some ventral-intercalary (never of *Microlepidozia*, *Acromastigum* or lateral-intercalary types). Leaf insertion usually distinctly succubous, rarely subtransverse, the orientation usually oblique; underleaves 0.35–0.7 the leaves in area 5

5a. Plants vigorous, 2.2–3.5 mm wide on sterile shoots; leaves imbricate, nearly covering stem (dorsal view), bearing (30)35–55 cilia or more; leaf lobes usually with (2)3–4(5–6) pairs of cilia; disc 12–16 cells high; cilia stiff, straight, those of disc margins never reflexed; perianth mouth cilia to 550–700 μm long; branches all of the *Frullania* type . . . . . *T. pulchellum* (p. 151)

5b. Plants small or medium in size, 1.2–1.9 mm wide; leaves distant or contiguous and allowing much of stem exposed, with (6)10–24 cilia, near gynoecia to 24–35(45) cilia; leaf lobes (sterile leaves) with 0–2 pairs of cilia; disc usually (5)6–12 cells high; cilia in part tortuous or recurved (at least the lowermost); perianth mouth cilia 175–450 μm long; some or most branches ventral-intercalary 6

6a. Leaf lamina strongly asymmetric, oblique, longer than wide, very unequally 4-fid; dorsal lobe small or obsolete, only 2–5 cells wide × 1–2 cells long, the other lobes also often small; lamina on mature leaves (5)6–8(9) cells high; cilia very long (to 800–835 μm) in relation to lamina, particularly on juvenile leaves, even on mature leaves longer cilia exceeding lamina in length; leaves rather concave adaxially, the cilia obliquely erect or ascending . . . . . *T. angustifolium* (p. 155)

6b. Leaf lamina essentially symmetrically obdeltoid to reniform-obtrapezoidal, wider than long (to apex of longest lobe), ± symmetrically 4-fid; lobes (mature leaves) triangular, (7)8–13 cells broad at base; lamina on mature leaves (8)9–11(13) cells high; cilia moderately long, the terminal cilia of mature leaves not longer than length of lamina (to lobe tip); leaves nearly flat, both lamina and cilia widely patent. Mature leaves ± reniform, usually strongly succubous . . . . . *T. paucisetigerum* (p. 154)

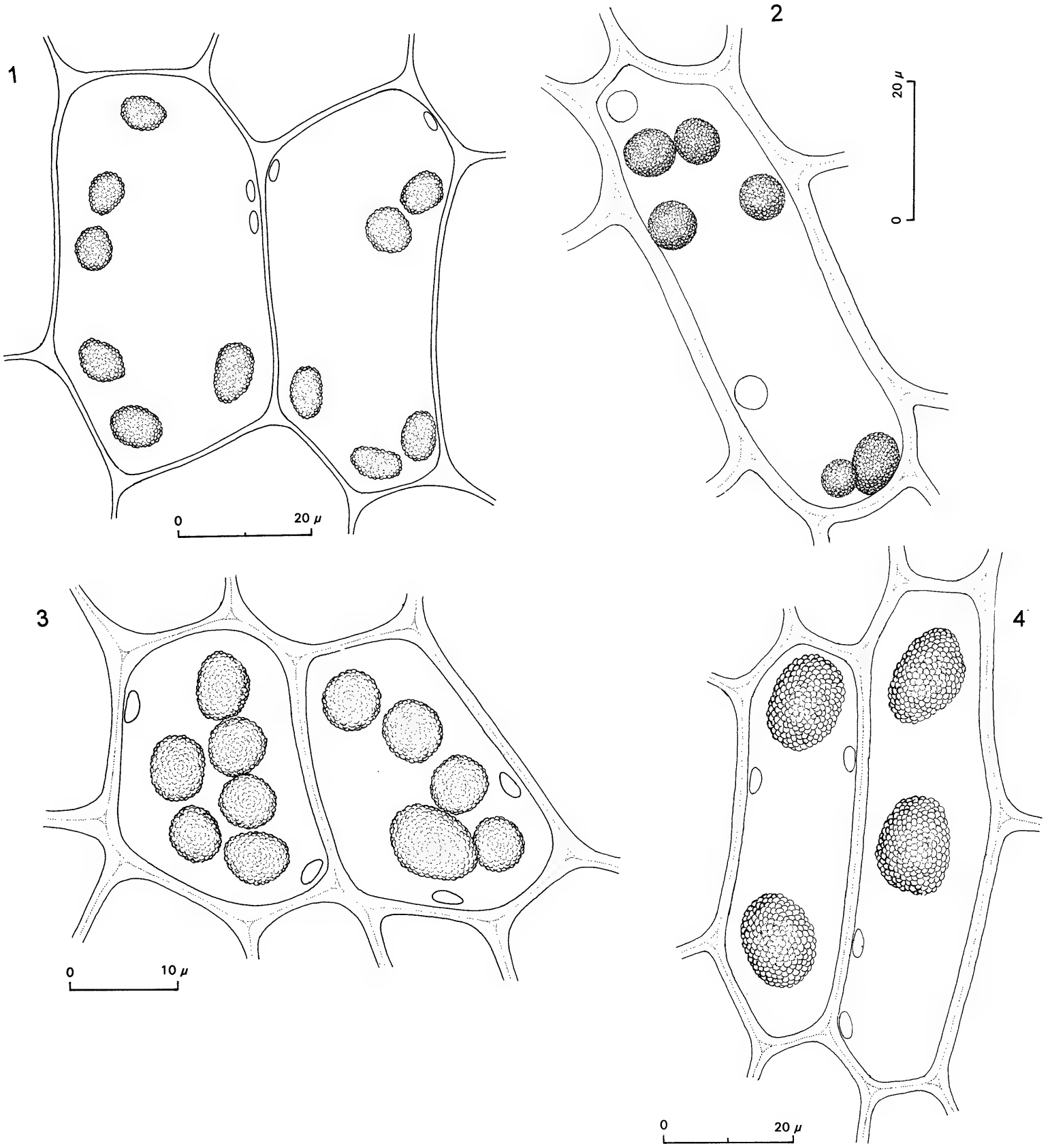

Fig. 20.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Temnoma pulchellum* (Hook.) Mitt. Median cells of disc. 2. *Temnoma paucisetigerum* R.M.Schust. Cells of disc. 3. *Temnoma quadripartitum* (Hook.) Mitt. Cells of disc. 4. *Temnoma quadrifidum* (Mitt.) Mitt. Cells of disc. (Fig. 1, from *Glenny 9266*, New Zealand, South Is., Western Nelson EP, Pupu Walkway; 2, from *Glenny 9008*, New Zealand, South Is., Westland EP, Griffin Ra.; 3, from *Glenny 9203*, New Zealand, South Is., Westland EP, Upper Otira Valley; 4, from *Glenny 8866*, New Zealand, South Is., Westland EP, Upper Otira Valley.)

Temnoma pulchellum (Hook.) Mitt.

[Plate 3A, B; Fig. 20: 1, oil-bodies, p. 150; Fig. 21]

Jungermannia pulchella Hook., Musci Exot. 1: *pl. 94*, *f. 1*–5. 1818. *Blepharostoma pulchellum* (Hook.) Steph., Sp. Hepat. 3: 640. 1909. *Temnoma pulchellum* (Hook.) Mitt. *ex* Bastow, Pap. & Proc. Roy. Soc. Tasmania 1887: 226. 1888 ("*pulchella*"). Type: New Zealand, South Is., Dusky Bay, 1791, *Menzies – c. per.* (G!, 2 coll.).

Plants with a woolly appearance, loosely creeping to suberect, green to yellowish brown; shoots robust, 2.2–3.5 mm wide, to 4 mm near apices of fertile shoots. Branches sparing, almost exclusively of the *Frullania* type, very rarely with isolated ventral-intercalary branches. Leaves of sterile shoots moderately imbricate, distinctly succubously inserted, 2000–2800 μm wide × 1500–1900 μm long (cilia included), obtrapezoidal to reniform, somewhat but not strongly asymmetrical, somewhat narrowed to the base, quadrilobed to 0.2–0.4 (uniseriate distal sector omitted), with a weak tendency for elaboration of an accessory lobe on the dorsal and ventral margins, the leaf as a whole (lobes and disc) with from 30–38 up to 50 cilia, depending on vigor of the plant. Lobes convex to sulcate, ± broadly acute, the margins sharply and conspicuously setose-ciliate (lobes each with [2]3–5[6] pairs of opposed cilia), the cilia stiff, glossy, 360–650 μm long, formed of generally 5–8 strongly elongated cells; cells of cilia thick-walled, rigid, smooth, 75–120 × 10–16 μm (in upper, tapering portions of cilia) to 22–25 μm wide (in lower portions of cilia); sinus bases ± reflexed, carrying basal cilia with them, which become abaxially recurved. Disc usually somewhat asymmetric, shorter at dorsal sinus than at ventral sinus, usually 12–16 cells high (sinus base to disc base); margins each with (2)3–5(6) long, stiff, straight, uniseriate cilia that are never recurved. Cells of lobes and undivided portions of leaves formed of slightly thick-walled, strongly elongated cells, partially aligned in regular tiers, the cells in the lobes and leaf middle 18–26 μm wide × (43)60–80(90) μm long; leaf surfaces nearly smooth to moderately verrucose. Oil-bodies in all leaf cells (including cells of the setiform lobe apices) occupying small portion of cell, dull, very pale grey, 5–9 per median disc cell, finely granular, subglobose to short-elliptic, 4.3–5.3 × 7.2–8.6 μm, spherical ones 6.7–7.2 μm in diam. Underleaves 0.5 the size of leaves, similar in shape to lateral leaves, quadrifid, the margins similarly spinescent. Fungal partner absent.

Androecia on leading shoots, becoming intercalary, somewhat more slender than vegetative portions of shoot; bracts closely imbricate, ventricose, somewhat spreading at base and the undivided portions then erect, only the 3–4 short lobes spreading to squarrose; lobes and margins near them strongly spinous-ciliate with setose cilia similar to those of the leaves; antheridia 1 per bract. Gynoecia on leading shoots. Bracts erect and sheathing the perianth, narrowly obtrapezoidal, 4(5–6)-lobed to 0.2, the margins of the lobes strongly reflexed (the lobes distinctly sulcate), setigerous or spinescent; lamina margins with 5–6 long cilia. Bracteole virtually like bracts. Perianth relatively elongated, at most weakly narrowed distally, terete below, strongly 3-plicate above, the plicae rounded, rather delicate, the mouth rather broad and truncate, densely setigerous and spinescent, similar to the leaf and bract margins; setose cilia and spines usually 60–70 per perianth mouth, polymorphous, the longer 550–700 μm long.

Seta with outer layer of cells in 19–20 rows of slightly larger cells that are distinctly collenchymatous, the inner core of cells in numerous rows, in 3–4 concentric tiers. Capsule ovoid-cylindrical, ca. 2–2.5× longer than broad, the wall 4–5 layered, ca. 40–50 μm thick; outer layer of cells very large, as thick or thicker than the two layers within combined, irregularly rectangular, pellucid, devoid of thickenings (except in 2[3] rows adjacent to sutures,

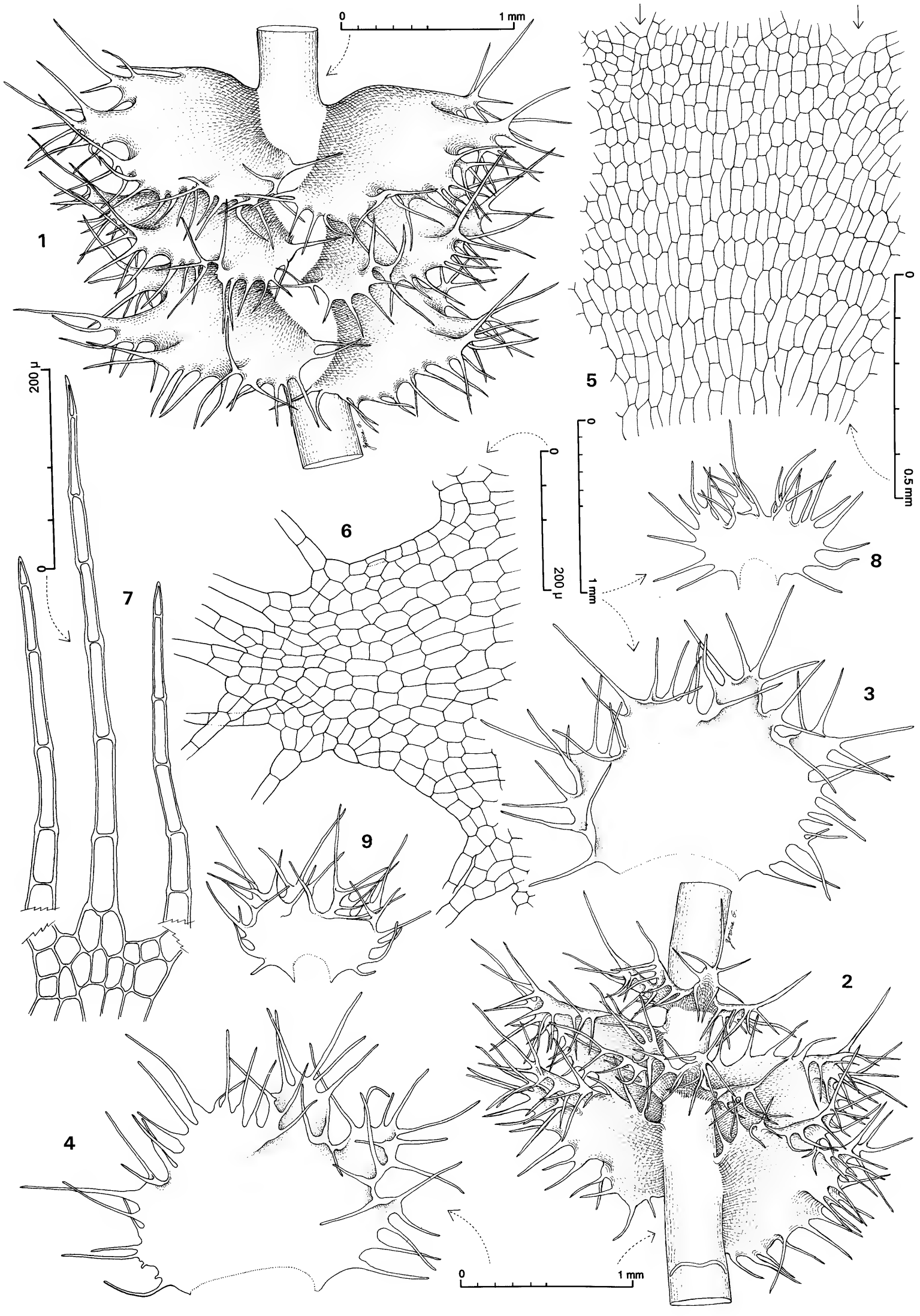

Fig. 21.
Temnoma pulchellum (Hook.) Mitt. 1. Portion of main shoot, dorsal view. 2. Portion of main shoot, ventral view. 3, 4. Leaves. 5. Sector through median portion of leaf disc, the sinus bases at arrows.

where with strong nodular to incomplete semiannular thickenings); innermost layer of cells very irregular, with numerous nodular to semiannular bands.

Spores translucent, pale brown, weakly verruculose, 8.5–9.5 μm in diam., subequal to that of elaters. Elaters rather sparingly produced, short and rather thick, bluntly pointed at the weakly tapering ends, 7.5–8.5 μm wide, somewhat contorted, closely bispiral, the reddish spirals ca. 3 μm wide.

Distribution and Ecology: Endemic to New Zealand: Stewart Island, South Island (30–500 m), North Island (340–1220 m). Known from Rakiura (Port Adventure, Port Pegasus), Fiordland (Garnock Burn), Southland (Bluff Hill), Westland (Ross, Lake Ianthe, Lake Ellery), Western Nelson (Karamea, Paparoa syncline), Southern North Island (Ruahine Ra.), Gisborne (Whirinaki), Auckland (Great Barrier Island, Coromandel Peninsula) and Northland (Waipoua, Trounson) EPs.

The species is sporadic in the South Island, where it occurs in dense wet forests on the floor (at times submerged in standing water), on boulders associated with stream courses or on rotted, decorticated wood. At one site it was on woody debris on a limestone wall. The species is common in damp forests of various types in the North Island and, in proper sites, may be locally abundant. It occurs, for example, at Waipoua Forest in *Quintinia serrata–Ixerba brexioides–Meterosideros umbellata* forests as well as *Agathis australis–Beilschmiedia* forests, and in podocarp–hardwood forests of *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*. Near creeks under secondary forest of *Fuchsia excorticata* and *Melicytus ramiflorus*. At higher altitudes found under *Libocedrus bidwillii* forest and *Nothofagus menziesii* forest. Commonly associated with *Canalohypopterygium tamariscinum*, *Distichophyllum pulchellum*, *Heteroscyphus billardierei*, *Ptychomnion aciculare* and *Rhaphidorrhynchium amoenum*. Other species that have been found with *Temnoma pulchellum* are *Achrophyllum quadrifarium*, *Cyathophorum bulbosum*, *Leiomitra lanata*, *Marchantia macropora*, *Metzgeria furcata*, *Plagiochila rutlandii*, *Radula dentifolia*, *Schistochila appendiculata*, *S. balfouriana* and *Weymouthia cochlearifolia*.

Comments: This species bears a slight vegetative resemblance to *Trichotemnoma corrugatum* (Steph.) R.M.Schust., but differs from it primarily in 1) the tiered leaf cells that uniformly lack trigones; 2) the presence of secondary (brown) pigments; and 3) the quadrifid underleaves (bifid in *Trichotemnoma*). The position and form of the gametangia, when present, will immediately distinguish the two: the androecia are subfoliose and intercalary on leading shoots in *Temnoma* vs. minute, bud-like, and ventral-intercalary in origin in *Trichotemnoma*. The gynoecia in *Temnoma* are on leading shoots vs. on short ventral-intercalary branches in *Trichotemnoma*.

This species has been confused with *Temnoma paucisetigerum*. *Temnoma pulchellum* is invariably found under forest while *T. paucisetigerum* is commonly found in more open habitats; the shoots of *T. pulchellum* are wider and the leaves denser.

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6. Leaf lobe (cilia not shown). 7. Distal portion of leaf lobe (the orientation of cilia artificially altered). 8, 9. Underleaves (drawn at same scale as leaves). (All from *Engel 17936*, New Zealand, South Is., Westland EP, between the confluence of Jackson R. and Arawata R. and Lake Ellery.)

Temnoma paucisetigerum R.M.Schust.

[Fig. 20: 2, oil-bodies, p. 150]

Temnoma paucisetigerum R.M.Schust., Candollea 21: 266. *f. 25–27.* 1967 (1966). Holotype: New Zealand, South Is., Fiordland Natl. Park, Hollyford Valley, Moraine Cr., 400–650 ft., *Schuster 48103* (herb. Schuster); isotype: (G).

Plants similar in general aspect to a small, remote-leaved, lax *Temnoma pulchellum*, but smaller in all its parts. Plants olive-brown to pale brown, the shoots 1.1–1.4(1.9) mm wide. Branches sporadic, of *Frullania* and, relatively frequently, ventral-intercalary types. Leaves remote or subcontiguous to weakly imbricate (less so than in *T. pulchellum*), somewhat succubously inserted, ± flat, perfectly symmetrical, reniform-obtrapezoidal, 1300–1750 μm wide × 1000–1450 μm long (including cilia), quadrilobed to 0.25–0.3 (uniseriate distal sector omitted), the leaf as a whole with (7)10–22 up to (in gynoecial plants) 24–30 cilia. Lobes plane to convex, 8–13 cells wide at base, each terminating in a ciliiform uniseriate row of (5)6–8(9) highly elongated cells, the cilia ca. (300)375–400(520) μm long, their length approximately the length of the lobe and disc below it, but never conspicuously exceeding it on mature leaves; longer cells of cilia 12–19 × 60–92 μm (4.5–6× longer than wide), thick-walled, the surface smooth or finely striolate; each lobe, in addition, with 0–2 pairs of cilia (the lowest situated near sinus bases and often abaxially displaced); sinus bases not or obscurely reflexed, not carrying cilia with them. Disc 8–13 cells high, much wider than long, lateral margins with 1–3(5) cilia, varying in length, the cilia in part ± tortuous or sinuous, the lowest sometimes recurved. Juvenile and suboptimal leaves symmetrical, with a reniform-obtrapezoidal disc that is shallowly quadrilobed and ends in 4 long, setose, terminal cilia, with occasional accessory ones developed. Cells slightly thick-walled, variable, on weaker leaves only short-oblong, in disc middle 16–26 × 28–52 μm to (20)25–30 × 40–65 μm; surface distinctly and closely striolate-papillose. Oil-bodies present in all leaf cells, but soon disappearing in tip cells of lobes, occupying small volume of cell, pale, smokey grey, 4–9 per cell in median sector of disc, faintly granular, most subglobose and 4.8–5.8 μm in diam., some elliptic (at times irregularly so) and 4.3–5.8 × 6.7–8.6 μm. Underleaves smaller, the disc shorter and broader, ± reniform to transversely oblong, usually quadrifid, sometimes trifid, each lobe ending in a long cilium.

♂ Plants more slender and with less freely ciliate leaves, the vegetative leaves reduced in size, the disc only obsoletely lobed. Androecia becoming intercalary, slender; bracts contiguous–imbricate, subequal to leaves in size, the base ventricose; lobes erect to suberect, terminating in setose cilia similar to those of the leaves, the dorsal margin of ventricose sector with spinose cilia. Gynoecial bracts erect, rather closely appressed to perianth, narrowly obtrapezoidal in basic outline, quadrilobed to ca. 0.2, the sinus bases and sides weakly or moderately reflexed; lobes pluriciliate, like leaf margins; lamina margins each bearing 1–5 stiff, short teeth or short cilia. Perianth ca. 0.5 emergent, bluntly trigonous, weakly contracted to the ciliate mouth; mouth bearing ca. 35–40 setose cilia of varying lengths, the longer 175–265 μm long, of ca. 5 superimposed cells. Spores 9–10 μm in diam. Elaters 8–10 μm in diam.

Distribution and Ecology: Endemic to New Zealand and rather widely distributed there, occurring on Campbell Island (250 m), South Island (80–1190 m) and North Island (600–1680 m). Known from Otago (Leith Valley, Taieri River mouth, Mt. Cargill, Maungatua, Flagstaff), Canterbury (Craigieburn Ra., Arthur's Pass), Westland (Lake Howden, Camp Creek, Paparoa Ra.), Marlborough (Branch River), Southern North Island (Tararua Ra.), Taranaki (Mt. Taranaki), Volcanic Plateau and Gisborne EPs, with a northern limit at Rotorua.

Occurring in various niches over a broad altitudinal range. In forests usually on soil, or thin soil over rocks, often in shaded, well-protected niches. In the alpine zone on soil, soil over rock, along rills, at stream edges and around pools; the species occasionally occurs on grass litter under *Chionochloa pallens* and *C. crassiuscula*. Associated species most commonly found with *Temnoma paucisetigerum* are *Balantiopsis tumida*, *Breutelia elongata*, *B. pendula*, *Ptychomnion aciculare*, *Riccardia colensoi* and *Trichocolea mollissima*. Other accompanying species are *Achrophyllum dentatum*, *Chiloscyphus spiniferus*, *Heteroscyphus sinuosus*, *Isotachis intortifolia*, *Lepidogyna hodgsoniae*, *Lepidozia pumila*, *Megaceros giganteus*, *Pachyschistochila colensoana*, *Philonotis scabrifolia*, *Plagiochila retrospectans*, *Pyrrhobryum mnioides*, *Riccardia pennata*, *R. pseudodendroceros*, *Sauloma macropora*, *Schistochila monticola* and *Triandrophyllum subtrifidum*.

Temnoma angustifolium R.M.Schust.

Temnoma angustifolium R.M.Schust., Candollea 21: 279. *f. 29*. 1967 (1966). Holotype: New Zealand, North Is., NW Ruahine Mtns., Otupae, Taihape, March 1934, *Hodgson 666* (herb. Schuster); isotypes: (MPN!, CHR ex herb. Allison H1956!).

Plants loosely prostrate to ascending to suberect, brownish, the shoots moderate in size, ca. 20 mm long, 1–1.8(2) mm wide. Branches sparing, irregular, of *Frullania* and ventral-intercalary types. Leaves of sterile shoots 1300–1800 μm wide × 950–1300 μm long (cilia included), by far the maximal area covered by the cilia, the disc relatively small, the leaves quite succubously inserted, weakly to moderately imbricate, usually rather concave, the lobes and the long cilia usually directed forward (the leaf orientation thus at times appearing subtransverse, in contrast to its insertion), normally very strongly asymmetrically 0.2–0.25(0.3) quadrilobed (omitting the uniseriate cilia), the dorsal lobe terminating in 1–2 cilia, the dorsal lobe often greatly reduced in size and frequently so reduced that the leaf approaches a trifid condition; total number of cilia per leaf ca. 18–21. Lobes asymmetric, the ventral two usually larger, ca. 4–6 cells wide at base, the dorsal often obscure and only 1–2 cells long and 2–3(5) cells broad at base, the lobes each ending in an extraordinarily long, setigerous uniseriate portion (650–835 μm long, and thus much longer than the leaf lamina lying below); cilia of lobe apices formed of up to 6–8 cells, the cells smooth, highly differentiated, linear, very thick-walled, up to 18 μm wide × 130–160 μm long (7–9:1), dilated at the septa; lobe margins each with at most (1)2–3(4) setose cilia; sinuses normally not or obscurely gibbous, without cilia (and thus without abaxially displaced cilia). Disc normally strongly asymmetrical, oblique, posterior margin much longer than the anterior, the width of disc (at level of apex of dorsal lobe) usually inferior to the length, the disc (5)6–7(9) cells high; lamina margins each usually with 1–2 long, setose cilia, the cilia often a little tortuous but usually not recurved, 330–500 μm long. Juvenile leaves with disc becoming greatly reduced, only 2–3 cells long × 6–8 cells wide, but the setose cilia very long, ca. 600 μm long, few (often only terminating the 4 lobes, the cilia otherwise usually 0–4). Cells of disc evenly, somewhat thick-walled, those in disc middle large, 25–30 μm wide × (45)55–65(70) μm long; surface strongly striolate-papillose. Underleaves smaller than lateral leaves, with greatly reduced disc, which is broadly reniform-obtrapezoidal, only ca. 3 cells high (to sinuses) and ± symmetrically quadrifid, each short lobe only 2–4 cells wide × 2–3 cells long; lobes each bearing 1–3 long, stiff, setose cilia, the terminal one longest (to 650–775 μm long, thus 4–5× the height of lamina; formed of 6–8 cells); cilia per underleaf as a whole ca. 10–14, occasional ones bifurcate.

Androecia on leading shoots, somewhat more slender than vegetative portions of shoot, 0.8 mm wide; bracts closely imbricate, ventricose, symmetrical, distinctly smaller than leaves, the lobes erect, reduced to cilia of a uniseriate row of 5 cells from a quadrate disc, the margins of ventricose sector also with short spinose cilia; antheridia 1 per bract. Gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (190 m), North Island (ca. 500 m). Known only from two sites, the type locality, probably in the gorge of the Taruarau River east of Otupae (Ruahine Ra.), and from the Tiropahi River (North Westland). The type collection was from "side of gorge," growing with *Heteroscyphus triacanthus*, *Symphyogyna undulata* and *Dicranella cardotii*. The South Island collection was on a limestone wall protected from direct rain under *Nothofagus menziesii* forest, and was growing with *Heteroscyphus triacanthus*, *Radula ?buccinifera* and *Marchantia pileata*. In both cases the plants were growing on plant debris, not directly on rock.

Temnoma quadrifidum (Mitt.) Mitt.

[Fig. 20: 4, oil-bodies, p. 150]

Jungermannia quadrifida Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 128. *pl. 94, f. 1*. 1854. *Blepharostoma quadrifidum* (Mitt.) Pearson, J. Bot. 25: 194. 1887. *Temnoma quadrifidum* (Mitt.) Mitt. *in* Hook.f., Handb. N. Zeal. Fl. 1: 753. 1867. Type: New Zealand, North Is., Patea Village, *Colenso 1117*.

Isotachis palmatiloba E.A.Hodgs., Rev. Bryol. Lichénol. 18: 30. 1949. *Temnoma palmatilobum* (E.A.Hodgs.) E.A.Hodgs. & Allison, Trans. Roy. Soc. New Zealand, Bot. 1: 146. 1962. Type: New Zealand, North Is., Kaimanawa Mtns., 4500 ft., Jan. 1947, *Druce* ("type no. 1062") (CHR, ex herb. K. W. Allison H4928!).

Plants erect to suberect, rather lax, green to yellowish brown to dark brown, almost black, the shoots medium or (rarely) small, (0.8)1–1.5 mm wide. Branches sparing to common, particularly from older plants and from ♀ shoots, variable, in large part ventral-intercalary (less often lateral-intercalary), other branches terminal, usually of the *Frullania* type, sometimes of *Acromastigum* and *Microlepidozia* types. Leaves exceptionally variable in form, size and degree of dentition, remote to (near shoot apex) imbricate, transversely oriented and inserted, exceptionally vaguely incubous, suberect to obliquely spreading, trapezoidal to obdeltoid or obdeltoid-obcuneate in outline, narrow at base and gradually broadened upward, palmately quadrifid to 0.5–0.6 (0.6–0.85 in middle sinus), the leaves often bisbifid, 750–1100(1800) μm wide at lobe apices × 700–1250 μm long. Lobes lanceolate-acute to lanceolate-acuminate, (4)6–15 cells wide at base, gradually tapering, usually ending in (1)2–4(5) superposed cells that are 17–26 μm wide × 20–30(40) μm long (1.2–2.5[3.5]:1); usually edentate, but 1 or 2 lobes occasionally with 1 (rarely 2) small, short, tapering teeth situated near or above lobe bases; sinus bases not reflexed. Disc (5)9–12 cells high, occasionally on vigorous, lax plants 14–17 cells high, edentate and without development of basal accessory lobes and usually with development of few or no accessory teeth or cilia. Cells slightly to moderately, evenly thick-walled, in median sector of disc from 17–24 × 35–50 μm to 22–28 × (44)48–75 μm; surface distinctly striolate-papillose. Oil-bodies in all leaf cells except the terminal cell of leaf lobes, large and conspicuous but occupying moderate portion of cell volume, dull, very pale grey, (1)2(3) in both disc and lobe cells, distinctly granular, the spherules tiny but well defined, the oil-bodies globose to very broad-elliptic, 9.1–11.5 × 11–13.4 μm, exceptionally more

narrowly elliptic and 7.2–8.2 × 11–13.4 μm, spherical ones 8.2–13 μm in diam. Underleaves very similar to leaves, somewhat narrower and more obcuneate, quadrifid or bisbifid to 0.5–0.6, the narrowly lanceolate segments usually in part entire, in part with 1–2 sharp to spinose marginal teeth.

Androecial shoots more slender than ♀ ones; androecia on main stems or elongate ventral-intercalary branches, laxly to compactly spicate; bracts similar to leaves but usually slightly smaller, transverse, less deeply and often somewhat asymmetrically quadrifid to 0.45–0.55, the lobes erect and not divergent, lanceolate, acute but not acuminate, entire-margined, the entire basal portion strongly ventricose and suberect, only the lobes suberect to widely spreading. Bracteoles smaller than underleaves and bracts, relatively shallowly (0.35–0.45) quadrilobed. Gynoecia with subinvolucral leaves and bracts gradually larger upward, progressively with margins bearing more frequent, often opposed, sharp teeth on lobes. Bracts erect, similar to leaves but larger, somewhat more freely dentate, broadly obcuneate to obdeltoid, bisbifid to 0.5–0.6, the lanceolate, long-acute to short-acuminate lobes varying from entire to sparingly toothed: the teeth 2–3(5) per lobe, the larger teeth broad-based, never aciculate, relatively short but sharp and formed of cells that are hardly differentiated from leaf cells, lying in the plane of the bracts, usually opposing. Bracteole similar to bracts. Perianth 0.5 or more emergent, the length 3–4× the width, tapering slightly from the basal third, where broadest; mouth rather wide, armed with remote to contiguous sharp teeth to short cilia (2–5, occasionally 6–8 cells long, the shorter uniseriate throughout, the longer tapering and 2–3 cells broad at base).

Capsule with nearly opaque valves, 4–5-stratose, from 35–36 μm thick (when 4-layered) to 41–46 μm thick (when 5-layered); outer layer of cells hyaline, rather large, devoid of pigmentation or localized thickenings (except near margins of valves, bordering dehiscence lines, and near or along the valve midline, where they are found with vertical bands or nodular thickenings; rarely a few cells elsewhere have sporadic thickenings along their longitudinal walls); intermediate strata each with strong vertical thickenings; innermost layer of cells usually less thick than intermediate cell layers, with numerous semiannular bands, the bands complete or subcomplete.

Spores 15–18.5 μm in diam., brownish, faintly but distinctly sharply papillate-granulate, the papillae not uniformly dispersed, the spores 2–2.5× the elater in diam. Elaters tortuous, 6.5–8 μm wide, strongly tapering on the ends, the spirals ca. 3 μm wide.

Distribution and Ecology: Endemic to New Zealand: Antipodes Islands (300 m), Stewart Island, South Island (30–1340 m), North Island (1370 m). Known from Rakiura (Tin Ra.), Fiordland (Mt. Burns), Southland (Eyre Mtns.), Canterbury (Danseys Pass, Temple Basin), Westland (Marks Flat, Otira River), Western Nelson (Pororari River, Stockton Plateau, Oparara River, Lake Peel), Taranaki (Mt. Taranaki) and Volcanic Plateau (Kaimanawa Ra., Mt. Ngauruhoe, Atiamuri) EPs.

Usually occurring on wet rock (schist, greywacke, granite), sometimes submerged in small cascading streams, often near waterfalls, or on ledges with seeping water, but sometimes on wet soil in bogs. Most commonly found in the penalpine zone (in *Chionochloa rubra* or *C. crassiuscula* tussockland or *Schoenus pauciflorus* sedgeland), but sometimes found under forest at lowland altitudes (e.g., *Dacrydium cupressinum – Nothofagus menziesii – N. fusca* forest at the Oparara and Pororari rivers). Commonly associated with *Bryum blandum* and *Cryptochila grandiflora*, but also found growing with *Blindia magellanica*, *Breutelia pendula*, *Chiloscyphus austrigenus*, *Dicranella cardotii*, *Fissidens rigidulus*, *Hepatostolonophora paucistipula*, *Isotachis intortifolia*, *Pachyglossa tenacifolia* and *Triandrophyllum subtrifidum*.

Comments: Plants that grow submerged are usually almost black, but those from lowland seepages may be golden brown, and these lowland plants show the greatest amount of toothing on the leaf margins. Very toothed forms may be confused with *Temnoma quadripartitum*, but lack the extra pair of lobes from the disc margins.

Temnoma quadripartitum (Hook.) Mitt.

[Fig. 20: 3, oil-bodies, p. 150]

Jungermannia quadripartita Hook., Musci Exot. 2: *pl. 117, f. 1–3*. 1820. *Temnoma quadripartitum* (Hook.) Mitt., J. Linn. Soc. Bot. 15: 68. 1876. *Blepharostoma quadripartitum* (Hook.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 417. 1877. Type: Argentina, Terr. Tierra del Fuego, Isla de los Estados, *Menzies*.
For extra-Australasian synonyms see Engel (1978, 1990a).

Plants usually rigid, rather wiry-stemmed, brownish to brownish green, usually scattered, exceptionally in small, nearly pure tufts, creeping to, with crowding, caespitose, small to medium, 0.8–1.2 mm wide. Branches sparing, irregular, usually of *Frullania* type, occasionally of *Microlepidozia* type, rarely ventral-intercalary. Leaves often rigid, small, remote to barely contiguous, the lamina stiffly, widely spreading, with ± suberect to ascending lobes, thus ± concave, the insertion ranging from transverse to somewhat succubous to (rarely) feebly incubous, the leaves obtrapezoidal to subquadrate-obtrapezoidal to obdeltoid to reniform-obtrapezoidal in outline, symmetrically quadrilobed to (0.6)0.75–0.85 (isolated leaves trifid). Lobes slenderly lanceolate-acute to ± gradually acuminate, (2)3–5 to 6(7–11) cells wide at base, the tapering apex formed by 3–5(7) cells in a row, the lobes rarely uniseriate nearly throughout (var. *pseudopungens*); lobes in basal half often with (0)1–2(4) pairs of spinescent, stiff teeth, the teeth often only in part opposing (the upper frequently solitary), never bifurcate, short above (and there only 1–3 cells long) and longer below (there sometimes 3–5-celled); teeth of lobes (particularly near the sinuses) sharply reflexed, ventrally displaced and lying almost at right angles to the leaf plane, in profile the plants thus appearing to have a stiffly spinose abaxial leaf surface; cells of teeth and lobe apices short, thick-walled (septa weakly dilated externally), 13–21 × 18–28 μm (weak phases) to 16–18 × 36–65(90) μm (vigorous phases), smooth to usually faintly, rarely strongly striolate. Disc only (2)3–5(7) cells high, occasionally 6–8 cells high on very vigorous plants; dorsal and/or ventral base with a tooth (widely spreading or reflexed) that is often larger than normal and is often large enough to suggest a 5–6-lobed leaf, or the margins with a few small teeth (var. *pseudopungens*). Cells of lobes and disc thick-walled (except basal cells of disc, which are sometimes leptodermous), the lobe cells 13–19 × 18–30 μm; surface smooth to faintly striolate-papillose. Oil-bodies occupying conspicuous volume of lumen, pale smokey grey, opaque, 3–6 per median disc cell, obscurely and indistinctly granular, with a hazy appearance, mostly subglobose, less often broadly elliptic. Underleaves distinctly smaller than leaves, otherwise like leaves but margins espinose or with mostly only 1(2) sharp, short teeth per lobe, quadrifid to 0.65–0.9, the disc (1)2 or 3–5 cells high, with one or both lateral bases often having a larger reflexed tooth.

Androecia intercalary (sometimes on rather short lateral branches), strongly differentiated; bracts very strongly concave, transverse, equal to or even slightly larger than leaves, much less deeply lobed than leaves and with shorter, usually erect lobes; margins of lobes spinose like the more spinose leaves, but disc bases without the large teeth of the leaves. Gynoecia with bracts erect, narrowly obtrapezoidal to cuneiform, gradually larger than leaves and becoming

much more spinescent, divided to ca. 0.6–0.75, the lobes linear-lanceolate, long-acuminate, ending in a filament of (3)4–6(8) isodiametric to ± strongly elongated single cells, often somewhat canaliculate, the lobe margins with 3–8(9) pairs of (generally abaxially reflexed) spinescent teeth per lobe; disc and lobe margins with spinescent teeth formed of (1)2–3 cells, those of the disc margins ca. 4–6 per margin. Perianth strongly elongate, strongly triplicate for 0.35–0.55 its length, distally with feeble accessory plicae, contracted to the mouth, which bears crowded, juxtaposed, short, stiff teeth and short cilia, strongly tapering to sharp points.

Spores 12 μm in diam. Elaters 7.2–9 μm wide, the spirals 2.5–3 μm wide.

The species may be subdivided into three varieties, all of which occur in New Zealand. These may be distinguished as follows:

Key to Varieties

1a. Leaves with lobes rigidly setaceous (of thick-walled cells), uniseriate except at the very base (there with vestigial bases 2–3 cells broad); ♀ bracts obtrapezoidal, the disc much wider than long, the lobes with 4–6 pairs of opposed, stiff teeth, the lobes each abruptly ending in a uniseriate terminal cilium longer than the lobe below . . . . . var. *pseudopungens* (p. 160)

1b. Leaves with lobes gradually tapering, the lobes 2 or more cells wide for most of their length (even on weak, juvenile stems); ♀ bracts narrowly obtrapezoidal-cuneiform, the disc no wider than long, the long-acuminate lobes each with 5–9 pairs of spinose teeth each, the apical uniseriate cilium shorter than the remainder of lobe below 2

2a. Lobes (3)4–5(6) cells wide at base, relatively abruptly narrowed distally, usually 12–17 cells long; disc margins rarely with accessory teeth so conspicuously lobe-like that the leaf is seemingly 5–6-lobed; lobe margins usually freely spinose-dentate toward base (miniature juvenile leaves excepted); surface feebly to distinctly roughened . . . . . var. *quadripartitum* (p. 159)

2b. Lobes either 3–4(5) or 6–8 (rarely to 9–11) cells wide at base, long-acuminate, gradually tapering, 16–22(30) cells long (on stem leaves); disc margins near or at base commonly with an enlarged spine that is lobe-like, often reflexed, the leaf seemingly palmately 5–6-lobed; lobe margins entire or with isolated, usually small (1–2[3]-celled) abaxially displaced teeth near sinus bases; surface smooth or nearly imperceptibly roughened . . . . . .var. *randii* (p. 160)

Temnoma quadripartitum (Hook.) Mitt. var. ***quadripartitum***

Leaves with lobes gradually tapering, (3)4–5(6) cells wide at base, 2 or more cells wide for most of their length (even on weak, juvenile stems); lobes relatively abruptly narrowed distally, usually 12–17 cells long; lobe margins usually freely spinose-dentate toward base (except miniature juvenile leaves); disc margin rarely with accessory teeth so conspicuously lobe-like that the leaf is seemingly 5–6-lobed; surface feebly to distinctly roughened; gynoecial bracts narrowly obtrapezoidal-cuneiform, the disc no wider than long, the long-acuminate lobes with 5–9 pairs of spinose teeth each, the apical uniseriate cilium shorter than the remainder of lobe below.

Distribution and Ecology: Amphi-Pacific temperate. New Zealand: Campbell Island (70 m), South Island (700–1140 m) and in the mountains of North Island (1280–1520 m); in the American sector in southern South America and the Falkland Islands. Also in the Subantarctic on Kerguelen Islands, Crozet Island, Marion Island and Prince Edward Island. In New Zealand in Fiordland, Westland (Clarke River), Canterbury (Huxley River, Mt. Cook Natl. Park, Arthur's Pass Natl. Park), Southern North Island (Ruahine Ra.) and Volcanic Plateau (Mt. Ruapehu) EPs.

On soil, in flushes, on stream banks and tarn margins, also in very constantly damp places on shady aspects of mountains, under penalpine scrub and low upper montane *Nothofagus solandri* var. *cliffortioides* forest as well as in *Chionochloa pallens* tussockland. Associated species are *Achrophyllum dentatum*, *Adelanthus occlusus*, *Balantiopsis tumida*, *Categonium nitens*, *Cephalozia* sp., *Chiloscyphus muricatus*, *Clandarium xiphophyllum*, *Conostomum pusillum*, *Dicranoloma robustum*, *Plagiomnium novae-zelandiae*, *Pyrrhobryum mnioides*, *Riccardia colensoi*, *Schistochila monticola*, *Trichocolea rigida* and *Tylimanthus diversifolius*.

Temnoma quadripartitum var. ***randii*** (S.W.Arnell) R.M.Schust.

Temnoma quadripartitum var. *randii* (S.W.Arnell) R.M.Schust., Candollea 21: 307. 1967 (1966).
Lepidozia randii S.W.Arnell, Svensk Bot. Tidskr. 47(3): 417. *f. 6*. 1953. Type: Marion Island, *Rand 3276*.

Leaves with lobes linear-lanceolate, gradually tapering, 17–22(25) cells long or more on mature leaves and terminating in (3)5–7 superposed single cells that are little elongated, the lobes (5)6–8(11) cells wide at the base; lobe margins of vegetative leaves entire or with an occasional tooth (rarely 2) per lobe, the teeth short, stiff, only occasionally abaxially displaced when present; disc base on one or both sides usually with a long, often tortuous or reflexed lobe-like lacinia; surface smooth or imperceptibly roughened.

Distribution and Ecology: The variety may represent a mere meso-hygrophytic extreme of *Temnoma quadripartitum* (Schuster, 1967a). The variety occurs in southern South America, Marion Island, St. Paul Island and one New Zealand station—along a watercourse at 1315–1435 m on Mt. Hector, Tararua Ra.

Temnoma quadripartitum var. ***pseudopungens*** R.M.Schust.

Temnoma quadripartitum var. *pseudopungens* R.M.Schust., Candollea 21: 312. *f. 36*: *9–10*. 1967 (1966). Type: New Zealand, South Is., Otago Prov., just S of Haast Pass, 1780–1810 ft., *Schuster 49649a*.

Leaves with lobes setaceous, the base consisting of only 2–3 laterally juxtaposed cells, the uniseriate distal sector usually 4–6 cells long, the cells of uniseriate row to 14–16 × 65–86 μm up to 15 × 90 μm; all or some lobes producing, at the base, 1–2 sharp, short, stiff, conical 1–2-celled teeth that are stiffly abaxially displaced; disc with 1–2(3)-celled marginal teeth that are never lobe-like (the leaf thus never incipiently 5–6-lobed).

Gynoecial bracts with lobes spinose-ciliate or spinose-dentate with 4–5 pairs of stiff, displaced (1)2–3(4)-celled teeth that are usually opposed, the lobes ending in long, setaceous apices formed of 5–8 superposed cells, which are 1.2–1.8× longer than the lobes themselves, the lobes thus caudate in aspect.

Distribution and Ecology: Known only from the type, occurring with *Adelanthus gemmiparus* and *Heteroscyphus cymbaliferus* on damp ledges along a small rill in a *Nothofagus menziesii* forest at ca. 550 m (South Island, New Zealand).

Temnoma palmatum (Lindb. *ex* Pearson) R.M.Schust.

Blepharostoma palmatum Lindb. *ex* Pearson, J. Bot. 25: 193. *pl. 275*. 1887. *Temnoma palmatum* (Lindb. *ex* Pearson) R.M.Schust., Bryologist 62: 240. 1959. Type: New Zealand, South Is., Otago, "inter *Hypnum rutabulum*," 1863, *Hector 13* (herb. Lindberg); Australia, New South Wales, Cambewarra, near Moss Vale, *Harris*.

Plants delicate, often rather lax and flaccid, erect to depressed-caespitose, bright green to somewhat pale yellowish brown, the shoots small, 0.6–1.5 mm wide. Branches rather sparse, variable, usually of *Frullania* type, less often of *Acromastigum* type, occasionally ventral-intercalary. Leaves suberect to rather spreading, distant to at most contiguous, sometimes weakly imbricate above, the insertion succubous, but mostly appearing nearly transversely oriented, the leaves subamplexicaul, obtrapezoidal in outline, narrow at the base, equally palmately quadrifid to (0.5) 0.55–0.65(0.75), without development of accessory basal lobes. Lobes lanceolate-acuminate, (3)5–9 cells wide at base 9–12(14) cells wide in aquatic phases, tapering gradually, each terminating in a uniseriate row of (2)3–6(8) cells, the uniseriate row variable: 85–200 to 490–655 μm long; cells of uniseriate row differentiated, usually 36–56(70) × 14–21 μm (ca. 2.5–3.5:1, rarely 4–5:1), except for the terminal, shorter, tapering cells; lobes of sterile shoots often eciliate; lateral lobes at base and/or upper margins of disc, at least on ♀ plants, with (0)1(3) additional, shorter, tapering teeth (1)2–3(4) cells long, the teeth usually lying in the plane of the leaf and not reflexed (except on ♀ plants). Disc often slightly concave, (5)6–12 cells high. Cells relatively pellucid, firm, generally somewhat thick-walled, those in disc middle 16–27(32) × (28)45–60(72) μm; surface delicately to strongly striate-papillose, even on the cilia (except in aquatic phases). Oil-bodies colorless, usually 2–4(5) per cell, up to (leptodermous phenotypes) 6–10(11) per cell, faintly granulate, smooth externally, spherical to irregularly ovoid, ca. 4.5–6.5 × 4.5–9 μm. Underleaves similar to leaves but smaller, often more deeply quadrifid, and with narrower lobes.

♂ Plants more slender. Androecia becoming intercalary; bracts smaller than the leaves, erect, clasping the stem, the disc ventricose, obtrapezoidal, quadrifid to the middle; lobes erect-spreading, subulate-lanceolate, entire or 1–2-dentate, ending in cilia 2–4 cells long. Gynoecia with bracts polymorphic, often somewhat similar to the upper leaves, moderately larger, cuneate to obtrapezoidal to subquadrate, quadrifid to 0.2–0.35 to 0.5–0.65, the narrowly lanceolate lobes with (1)2–4(6) pairs of ± opposed sharp, slenderly spinose teeth or cilia, those of the lobe bases usually ± reflexed. Bracteole almost identical to bracts in shape and size. Perianth (xeromorphic forms) rather short, at maturity distinctly, often long-stipitate, ovoid to obconical to short-tubular, slightly and irregularly crispate and plicate in the distal 0.2–0.25, at times obtusely and obscurely trigonous above, the mouth ± wide, subtruncate, irregularly lobulate and laciniate-ciliate; hygric forms with perianth prismatic, long, not stipitate; mouth with teeth relatively few and often distant, to 20–30, similar to the teeth of the leaves: variable, irregular in size and orientation, usually formed of 2–5 superposed cells (which may arise directly from small lobes).

Seta varying according to the vigor of the plants (within one clone): in weak plants with only 13–15 rows of outer cells that are considerably larger in diameter than the 12–13 rows

of internal cells; larger plants the seta with 16–18 rows of outer cells that average only slightly larger than the ca. 22 rows of internal cells. Capsule short-ellipsoidal, the wall 3–4 stratose, 26–29 μm thick; outer layer of cells colorless and hyaline, very large, 13–15 μm high; intermediate strata with well-defined, strong, nodular thickenings; innermost layer of cells very irregular, the walls with ± sharply defined nodular thickenings (of all longer walls, both longitudinal and transverse), which are often tangentially extended to varying degrees (but are only locally and often sporadically complete forming semiannular bands).

Spores 9.4–11.2 μm in diam., yellow-brown, feebly punctate-granulate. Elaters strongly contorted, with curved to hooked, narrowed apices, 6.5–7.2 μm wide, bispiral (exceptional elaters unispiral), the spirals closely twisted, ca. 2.5 μm wide.

Key to Varieties

1a. Leaves divided to 0.5 their length, the lobes not or scarcely longer than disc; surface smooth or papillose. Perianth (where known) prismatic, long and ± slender, not stipitate and elevated above the bracts, somewhat contracted to mouth, with long cilia at mouth (to 400–410 μm long), formed of 5–6 cells. ♀ Bracts (where known) divided to 0.2–0.35(0.4), oblong-cuneate to cuneiform-obtrapezoidal, 2.1–2.5× as long as wide. Oil-bodies from 6–11 per cell 2

2a. Leaves (♂ plants) with disc 9–12(14) cells high; lobes long-acuminate, ending in 7–8 cells; lobe bases 8–12(14) cells wide; surface smooth or indistinctly papillose. Leaves of sterile shoots with 1–2(3) cilia per lateral margin of disc . . . . . var. *laxifolium* (p. 164)

2b. Leaves (♂ and ♀ plants) with disc 7–9 cells high; lobes short-acuminate, ending in 3–5(6) cells; lobe bases 7–9 cells wide (on leaves below gynoecia to 10–12 cells wide); surface papillose. Leaves of sterile shoots with 0–1(2) cilia per lateral margin of disc . . . . . var. *cuneatum* (p. 164)

1b. Leaves divided to 0.75 their length, the lobes (including cilia) normally much longer than disc; leaf surfaces always strongly papillose. Perianth normally short, long-stalked and seemingly elevated above bracts, wide and ± crispulate at the mouth, armed with teeth or short cilia (to 200–240 μm long) formed of 2–5 cells. ♀ Bracts divided to 0.45–0.6, ± narrowly obtrapezoidal to subquadrate. Oil-bodies 2–6(7) per cell 3

3a. Leaves (sterile plants) with lobes ± reduced, narrow, only 2–4(6) cells broad at base, rather abruptly narrowed into the differentiated terminal setae. ♀ Plants, even on smaller leaves, with 1–several abaxially displaced, short, rigid, spinescent teeth of the sinus bases. Perianth mouth long- and stiffly ciliate (cells ca. 4.8:1), and (in part) with reflexed cilia or teeth, with to usually 30–48 teeth. ♀ Bracts narrowly obtrapezoidal. Oil-bodies (2)3–6(7) per cell . . . . . var. *pseudospiniferum* (p. 163)

3b. Leaves with lobes well developed, the larger usually 5–9 cells broad at base, gradually narrowed into ill-defined terminal cilia. All plants, ♂ and ♀, with sinus bases lacking displaced, spinescent teeth (except in vicinity of gynoecia). Perianth mouth with fewer short to moderately well-developed cilia. ♀ Bracts often broadly obtrapezoidal to subquadrate. Oil-bodies 2–4(6) per cell . . . . . var. *palmatum* (p. 163)

Temnoma palmatum (Lindb. *ex* Pearson) R.M.Schust. var. ***palmatum***

Leaves usually quadrifid to 0.6–0.65(0.75), the lobes slenderly lanceolate, (4)6–9 cells wide at the base, usually lacking cilia, on larger leaves occasionally with 1(2) teeth at the lobe bases, the lobe apices short-acuminate, formed of 3–5(6) superposed cells; disc relatively low (height always inferior to length of lobes), up to a maximum of 7–9(10) cells high. Leaf surfaces distinctly verrucose or papillose. Oil-bodies rather large for cell size, (2)3–5(6) per cell, 4.5–6.5 × 4.5–9 μm.

♀ Bracts variable, ± subquadrate, 4(5)-fid to 0.5–0.6(0.65); lobes with cilia unequal, from 1–2 to 4–5(6) pairs per lobe. Perianth normally ± reduced, slenderly ovoid to ovoid-campanulate, ± crispulate-lobulate at mouth, the mouth armed with short, spinose teeth or cilia to 2–4 cells long usually; with maturation a long neck usually develops from elaboration of receptacular tissue, elevating the perianth on a stipe often equal in length to the perianth proper; the 3 bracts, widely separated, occur on this stipe.

Distribution and Ecology: New Zealand: Campbell Island, South Island (600–1540 m), North Island; Australia: New South Wales. Known from Fiordland (Lake Manapouri, Takahe Valley), Otago (Dunstan Mtns., Naseby, Remarkables), Westland (Upper Otira River valley), Canterbury (Upper Bealey valley, Danseys Pass), Southern North Island (Ruahine Ra.) and Gisborne (Wairoa) EPs.

According to Schuster (1967a, p. 342), the variety often occurs "in open, insolated areas where it is subject to drying out; here found occasionally associated with Manuka (*Leptospermum scoparium*)." In moist sites occurring on thin soil over limestone (Ruahine Ra.). In the Otira River valley it was found under a soil overhang next to a stream, with *Balantiopsis convexiuscula*, *Breutelia pendula*, *Ditrichum punctulatum*, *Lepidozia obtusiloba*, *Riccardia crassa* and *Triandrophyllum subtrifidum*. In Central Otago it was in an alpine cushion bog on the edge of a stream, with *Allisonia cockaynei*, *Bryum laevigatum*, *Clasmatocolea strongylophylla*, *Riccardia bipinnatifida*, *Syntrichia robusta* and *Warnstorfia fluitans*.

Temnoma palmatum var. ***pseudospiniferum*** R.M.Schust.

Temnoma palmatum var. *pseudospiniferum* R.M.Schust., Candollea 21: 348. *f. 26*: *4–6, 48*: *8–12, 50*: *3*. 1967 (1966). Type: New Zealand, North Is., NW Ruahine Mtns., Otupae, *A. P. & H. M. Druce* (MPN, ex herb. Hodgson 3525; herb. Schuster; CHR ex herb. Allison H5262!).

Plants with an aspect approaching that of *Temnoma quadripartitum*. Leaves usually quadrifid to 0.6–0.65, the lobes of mature leaves with lamina reduced, only 3–4(5) cells broad at base, on larger leaves (♀ plants) often with a pair of teeth per lobe that are 1–3 cells long and spinescent, situated at the sinus bases and sharply postically displaced, not lying in leaf plane; lobes setaceous, each ending in a well-differentiated apical spine formed of to 6–7 superposed cells (3–5:1); disc low (height always slightly to much inferior to lobe length), usually only 6–7 cells high; disc margins on each side with (0)1–2 short to long, spinose teeth or cilia. Cells with surface rough. Oil-bodies 4–6(7) per cell, 4–6 × 5–7 μm, or spherical and 4.2–5.5 μm in diam. Gynoecial bracts initially forming, with the bracteole, a spinescent, thistle-like capitulum, with development of sporophyte becoming widely separate. Bracts narrowly obtrapezoidal, quadrifid to 0.3–0.45, the lobes copiously long-spinescent to ciliate, each lobe with 2–3(4) opposed pairs of setose cilia formed of 2–3(4) thick-walled, strongly elongated cells;

apices of lobes setaceous, the uniseriate row to 300–400 μm long, formed of 4–5(6) strongly elongated, highly differentiated cells; sinus bases and some spinescent, rigid cilia originating there, sharply reflexed. Perianth relatively abbreviated, strongly stipitate at maturity and elevated above bracts, ovoid-ellipsoid, subterete and hardly perceptibly trigonous, inflated, the base narrowed, the mouth armed with 24–48 stiff, setose, variable cilia and spines, the armature ranging from mere spines 1–2 cells long (usually under 200 μm long) to long bristles 300–450 μm long, then formed of 4–6 thick-walled, very elongated cells.

Distribution and Ecology: Known only from a few stations in the North Island (NW Ruahine Ra. and near Taupo) and in the South Island from a few stations in Southland and Otago (500–1000 m). In the latter area it may occur on bark of *Nothofagus menziesii*. At Wye Creek it occurred on soil on the stream bank under *N. solandri* var. *cliffortioides* forest with *Leptophyllopsis laxus* and *Megaceros pellucidus*.

Temnoma palmatum var. ***laxifolium*** R.M.Schust.

Temnoma palmatum var. *laxifolium* R.M.Schust., Candollea 21: 345. *f. 45*: *1*, *46*. 1967 (1966). Type: New Zealand, Stewart Is., Tin Range, N of Pegasus, ca. 1000 ft., *Schuster & Scott 49981* (herb. Schuster, G, S-PA, NY).

Plants very soft-textured and lax. Leaves not at all spinescent, usually quadrifid to 0.5–0.6; lobes lanceolate, broad-based, 8–12(14) cells wide at the base, gradually long-acuminate, ending in a setiform uniseriate row of up to 7–8 elongated (2.8–5:1) cells; lobes usually quite free of cilia; disc (8)9–12(14) cells high, obtrapezoidal, the lateral margins bearing 1–2(3) slender, often long, tapering cilia on each side. Leaves and underleaves near androecia more copiously ciliate-dentate but hardly spinescent. Cells with surface indistinctly papillose. Oil-bodies small for size of cell, (6)7–9(10) per cell, 4.4–4.8 μm and spherical to ellipsoidal and 3.8 × 7.5 to 3.5–5.5 × 4.5–6 μm.

Distribution and Ecology: Known only from Stewart Island and Otago and Westland Prov. in South Island, New Zealand. It is aquatic to subaquatic, occurring in shallow, flowing rivulets or boggy niches in open areas (300–1170 m).

Temnoma palmatum var. ***cuneatum*** R.M.Schust.

Temnoma palmatum var. *cuneatum* R.M.Schust., Candollea 21: 347. *f. 47*. 1967 (1966). Holotype: New Zealand, South Is., ca. 1.5–2 mi. S of Wilmot Pass, between Lake Manapouri and Doubtful Sound, N of Spey River, ca. 1500 ft., *Schuster 52661* (herb. Schuster).

Leaves usually 0.5–0.55 quadrifid; lobes slenderly lanceolate, usually 5–9 cells broad at base (some lobes of leaves of ♀ plants to 10–12 cells broad), the lobes normally edentate (♂ plants), or on ♀ plants with at most 1(2) non-recurved teeth near the base; lobes gradually tapered, with apices short-acuminate, formed by usually 3–5 superposed, elongated cells (3–5:1); disc 7–9 cells high, appearing as high as the lobes are long, with 0–1(2) spinous teeth on each side. Cells with surface conspicuously papillose. Oil-bodies 7–10(11) per cell, rarely and sporadically 5–6 per cell, 4.5–6 × 6–7.5 μm.

♀ Bracts cuneiform to oblong-cuneiform, 0.2–0.35 quadrilobed, the lobes each with usually 2–3 pairs of small, spinose uniseriate teeth mostly 2–4 cells long; disc high and very narrow.

Perianth long, not or obscurely stipitate, prismatic, sharply trigonous almost throughout, somewhat contracted to the mouth, which is conspicuously and densely long-ciliate (cilia up to 350–410 μm long, formed of up to 5–6 superposed cells).

Distribution and Ecology: Known from a limited suite of specimens in New Zealand. In the South Island occurring in Southland over a wet, shaded rock, in a site on a mountain slope (300 m) where inundation could not occur. In the North Island occurring on Mt. Taranaki at 1650–1675 m on cliff faces and rocks in an herbfield in the alpine zone (Schuster, 1967a).

Archeophylla R.M.Schust.

Archeophylla R.M.Schust., J. Hattori Bot. Lab. 26: 263. 1963.

Plants moderately to distinctly anisophyllous, creeping or procumbent (ours) to ascending to erect, ± rigid, green to pale brown to yellow-brown. Branching sparing, irregular, the branches nearly always ventral-intercalary; terminal branches present, sporadically of *Frullania* type, rarely of *Microlepidozia* type. Stems stiff and wiry, the cortical cells with exposed wall thickened, moderately to distinctly larger than the medullary cells; medullary cells firm-walled, thickened at the angles. Rhizoids frequent, from underleaf cells. Leaves remote, widely spreading (in ours), the insertion transverse to feebly succubous, broadly obcuneate to obtrapezoid, equally 3–4-lobed to (0.55)0.6–0.75(0.8) (never bisbifid); lobes long-acuminate, only 2–4 cells wide at base, tapered distally to a setaceous uniseriate row of 7–13 cells, the lobes entire (rarely with a tooth on trifid leaves); disc 5–7 cells high, the cells at most slightly elongated (at most 2× longer than wide), the margins entire or (ours) at times with a tooth. Cells with walls firm and with trigones somewhat bulging or (ours) markedly nodose, confluent or separated by narrow, thin-walled places; cell surface smooth (ours) or papillose-striolate. Oil-bodies (Schuster, 1966a) (1)2–3(4) per cell, greyish, granular. Underleaves 0.4–0.75× lateral leaves but otherwise similar in form, (2)3–4-lobed, lobes stiff, setaceous, uniseriate throughout or with 1–2 biseriate tiers at base; disc 2–5 cells high. Asexual reproduction absent, or by fragmentation of leaf lobes.

Dioecious. Androecia on leading shoots or ± short *Frullania*-type branches, distinctly differentiated, compactly spicate, the bracts in only (1)2–4(5) pairs; bracts less deeply lobed than leaves (0.5–0.6), the entire disc strongly ventricose, the lobes setaceous, erect to suberect, the bracts monandrous; bracteoles smaller. Gynoecia terminal on long shoots; bracts in 2–4 series, becoming gradually larger but the innermost series usually smaller; bracts of innermost series variable, erect and sheathing base of perianth, 3–4-fid to 0.35–0.55; lobes slenderly acuminate-setaceous, not or at most weakly divergent, entire or with 1–3(4) non-opposed spinose teeth toward base (the teeth only occasionally opposed in *Archeophylla pungens*); bracteoles similar to bracts but smaller. Perianth long-exserted, lacking a coelocaule-precursor at base, terete below, distinctly 3-plicate in distal 0.25–0.65, contracted to the mouth; mouth lobulate-ciliate, the cilia stiff, bristle-like, long, crowded.

Capsule ovoid, the wall 3–4-layered; outer layer of cells high, with small, remote, nodular thickenings (in *Archeophylla pungens*) only in cells adjacent to valve margins; innermost layer with nodular to spine-like thickenings (occasionally tangentially extended into local complete semiannular bands in *A. pungens*).

Spores finely to coarsely papillose. Elaters strongly tortuous, short, the tips strongly and abruptly attenuated, unispiral, the spiral exceptionally wide (7–10 μm).

Type: *Archeophylla schusteri* (E.A.Hodgs. & Allison) R.M.Schust (≡ *Temnoma schusteri* E.A.Hodgs. & Allison)

The genus includes only our species, the generic type and two from southern South America, *Archeophylla pungens* (Herzog) R.M.Schust. and *A. paradoxa* R.M.Schust.

References: Schuster (1966a, rev.; 2000a).

Treatment of genus adapted, with considerable modification, from Schuster (1966a).

Archeophylla schusteri (E.A.Hodgs. & Allison) R.M.Schust.

[Plate 3C; Fig. 24: 1, oil-bodies, p. 178]

Temnoma schusteri E.A.Hodgs. & Allison, Trans. Roy. Soc. New Zealand, Bot. 1: 147. 1962. *Archeophylla schusteri* (E.A.Hodgs. & Allison) R.M.Schust., J. Hattori Bot. Lab. 26: 263. 1963. Holotype: New Zealand, Stewart Is., Table Hill, *Martin 481* (MPN, "sub number 9355 Herb. E. A. H.").

Plants subisophyllous, creeping to (rarely) erect, usually as single isolated shoots, at best loosely gregarious, light green to pale brown; shoots small, 10–15(25) mm long, to 1.5–1.6 mm wide with leaves but often smaller. Branching sparing, remote, the branches nearly uniformly ventral-intercalary, sporadically of *Frullania* type, rarely *Microlepidozia* type. Stems sinuous, brownish, the cortical cells in 10–16 rows, not tangentially flattened, the exposed wall strongly and evenly thickened; medullary cells in 8–12 rows. Rhizoids frequent. Leaves obliquely to widely spreading, at times squarrose, plane to weakly concave, palmately (2)3–4-lobed to 0.65–0.8, 780–930(1050) μm wide × 600–800 μm long; lobes markedly diverging, entire, 2–4 cells wide at base, terminating in a uniseriate row of 9–13 cells; cells of the uniseriate portion gradually becoming longer and narrower, those toward base of uniseriate row not much longer than wide, those at lobe tips 10–11 × 50–58 μm, decolorate, the cells of uniseriate row markedly thick-walled; disc (5)6–7(8) cells high, the margins entire or with a small tooth, often on the dorsal margin. Cells with a distinct, yellow-brown middle lamella, the trigones colorless, coarse, nodose, sometimes confluent, the thin-walled areas between cells narrow, almost pit-like; cells of disc 23–29 × (25)30–38(52) μm, often oblong-polygonal, never clearly rectangular; cell surface smooth. Oil-bodies occupying conspicuous portion of cell lumen, at times nearly filling the lumen, pale smokey grey, 2–4 per lobe cell, 2–3 per disc cell, coarsely granular, globose to broadly ovoid to short broad-elliptic. Underleaves (2)3–4-lobed, at times all 4-lobed, one or both lateral lobes often abbreviated; lobes 9–13 cells long, uniseriate throughout or biseriate at extreme base; disc 3–5 cells high.

Androecia with bracts strongly inflated, the lobes setaceous. Gynoecia with bracts in 2–3 series, the lower 1–2 series usually clearly larger than those of innermost series, those of the lower series with suberect bases but stiffly spreading to squarrose, ± tortuous-recurved lobes; bracts of innermost series variable, erect throughout and ensheathing the perianth base, deeply 3–4-fid, the lobes long, tapered, acuminate, with 1–2(3) stiff, sharp teeth or short usually alternate cilia; disc obtrapezoidal; bracteoles of innermost series smaller than bracts, often only 2–3(4)-fid, sparingly armed with non-opposed spinose teeth. Perianth 3-plicate in distal 0.25–0.3(0.5), contracted at the ± closed, often decolorate mouth; mouth lobulate-ciliate, the cilia crowded, with a uniseriate row of up to 5, thick-walled, somewhat elongated cells.

Capsule wall 3–4-layered, the outer layer of cells with nearly all longitudinal and some transverse radial walls with rather weak nodular to spur-like thickenings; innermost layer of cells with weak nodular to local spur-like thickenings, with semiannular bands lacking.

Spores (Schuster, 1966a), 12–15 μm in diam., rather coarsely papillose, the papillae well spaced. Elaters strongly tortuous, 7–8 × 60–95 μm, the single spiral 8–10 μm broad.

Distribution and Ecology: Endemic to New Zealand: Campbell Island (70 m), Stewart Island (30–?400 m), South Island (185–1200 m), North Island (ca. 1200 m), Chatham Islands (160 m). On Stewart Island known from Table Hill, Tin Ra. and Pegasus Creek. In the South Island known from Belle Vue Island (Lake Manapouri, Fiordland EP, 185 m), Sewell Peak and Gordon Creek (both Paparoa Ra., Western Nelson EP), Mt. Bell (Marino Mtns., Western Nelson EP), and Mt. Patriarch and Porter Rock (both Arthur Ra., Western Nelson EP). In the North Island known only from the southern slopes of Mt. Ruapehu (Blyth Track and Mangawhero River, Volcanic Plateau EP).

A plant of peaty, mossy mounds or banks, at times under old stands of *Leptospermum scoparium* and for the most part in relatively open sites that are either well-illuminated or in niches that are protected and permanently damp but never flooded. Along the Blyth Track (Tongariro Natl. Park), plants occurred loosely gregarious in a thick mound of bryophytes on the side of a log near a small stream in a rather open *Nothofagus solandri* var. *cliffortioides* forest (ca. 1230 m). At Sewell Peak it was found under *N. solandri* var. *cliffortioides – Halocarpus biformis* forest on an old log. On Mt. Patriarch it was found under low *N. menziesii – Archeria traversii* forest near treeline, in a cushion of *Anastrophyllum schismoides*. On Chatham Island it was in cushions of *Dicranoloma robustum* and *Anastrophyllum schismoides* under semi-open *Dracophyllum scoparium* shrubland. Plants appear to always occur over organic material, and for the most part peat. Plants usually occur as single, isolated, straggly stems or they are at most loosely gregarious. *Archeophylla schusteri* must be carefully searched for, and is likely to be found sparingly admixed with other bryophytes, particularly among *Acromastigum anisostomum*, *A. mooreanum* and *Eotrichocolea polyacantha.* Other species that it has been found with are *Acrobolbus lophocoleoides*, *Anastrophyllum schismoides*, *Bazzania adnexa*, *B. involuta* var. *submutica*, *Chiloscyphus leucophyllus*, *Dicranoloma billardierei*, *Gackstroemia alpina*, *Heteroscyphus decipiens*, *Hymenophyllum armstrongii*, *Lepidozia kirkii*, a *Leptoscyphus* sp. and *Trichotemnoma corrugatum.* On Campbell Island it occurs on peat in open shrubland, with *Adelanthus occlusus*, *Marsupidium surculosum* and *Riccardia perspicua.*

Comments: *Archeophylla schusteri* is a distinctive plant. The species typically occurs as isolated, wispy shoots and is almost *Telaranea*-like in superficial aspect or like a very small *Temnoma*. However, it may be immediately differentiated by the strongly nodose trigones, a character that will separate it from all other *Pseudolepicoleaceae* (and from *Telaranea* as well). Also distinctive are the deeply 3–4-lobed, widely spreading to squarrose leaves with markedly attenuated, entire lobes. The lobes terminate in a uniseriate row of 9–13, notably thick-walled cells. The disc margins are entire or they may have a small tooth, often on the dorsal margin.

Family **TRICHOCOLEACEAE** Nakai

Trichocoleaceae Nakai, *in* Ogura, Ord. Fam. Trib. Gen. Sect. ... nov. ed. 200. 1943.

Plants often appearing like a mass of interwoven hairs, anisophyllous, usually prostrate, at times pendulous, pale green to yellow-green to pure green, lacking secondary pigments (except *Castanoclobos*); plants small to robust. Branching for the most part regularly 1–3(4)-pinnate

(except *Castanoclobos* and *Leiomitra*), the branches nearly exclusively of *Frullania* type; *Acromastigum*-type branches rare or sporadic (*Leiomitra* and *Eotrichocolea*); intercalary branches lacking. Stems often copiously paraphyllose, the cortex poorly differentiated. Rhizoids absent or rare, sometimes from a unistratose rhizoid pad on the underleaf lamina. Leaves often highly dissected into lobes and cilia, with insertion usually succubous (± transverse to incubous in *Eotrichocolea*), asymmetric, the ventral lobes larger and the ventral sector of disc higher, deeply (3)4-lobed, but often with numerous secondary, smaller lobes; lobes acute to acuminate, usually narrow, usually armed with often branched, typically opposed cilia, the cells of lobes and cilia elongate; disc usually low, of only a few cells high. Cells of disc elongate-rectangular, often ± in tiers, thin- or weakly firm-walled; surface papillose or striate-papillose. Oil-bodies 4–14 per cell, up to 33 per cell in cilia, spherical and 3.5–6 μm diam. or 3.5–6 × 7–8 μm and irregularly ovoid, or ellipsoidal, grey, finely granular to papillose. Underleaves symmetric, bifid, but the lobes again divided (except *Eotrichocolea*), often bisbifid, armed as in leaves. Asexual reproduction lacking.

Dioecious. Androecia on leading leafy shoots; bracts concave, basically similar to leaves but with lamina larger and lobes shorter, with 1–2 antheridia, the stalk biseriate (?always); bracteoles without antheridia. Gynoecia on leading leafy shoots in ours (on short, *Frullania*-type branches in *Leiomitra* subg. *Brachygyna*); bracts and bracteoles similar to leaves and underleaves but larger and more freely lobed. Sporophyte protected by a bulbous to clavate coelocaule densely covered by reduced bracts and paraphyllia, commonly hispid in aspect; perianth completely absent (*Trichocolea*, *Eotrichocolea*), or present as a low, deeply lobed remnant (*Leiomitra*), or well developed, fused to and continuous with a perigynium and invested in hairs (*Castanoclobos*); calyptra absent or (*Leiomitra*) present and low, cap-like or bulbous.

Seta of numerous cells, the outermost and internal cells ± similar in size. Capsule ellipsoidal, ovoid or spherical, 3–8-layered, the outer layer of cells hyaline, high, with pigmented wall thickenings absent or sparse; innermost layer of cells with small nodular thickenings, at times with incomplete or complete semiannular bands.

Spores granular or granular asperulate. Elaters sinuous, not tortuous, bispiral or less often 3-spiral or 2–3-spiral.

Type: *Trichocolea* Dumort.

A family with four genera, all of which occur regionally. It includes some of the most beautiful and intricate of hepatics, including the recently described *Castanoclobos*.

Castanoclobos J.J.Engel & Glenny

Castanoclobos J.J.Engel & Glenny, Novon 17: 424. 2007.

Plants spongy, distinctly julaceous, with all sides appearing as a mass of interwoven cilia, loosely creeping, chocolate-brown (the shoot tips light green), the shoots to 2 mm wide. Branching irregularly sympodial to pseudodichotomous, the leading axis soon losing its dominance, the main shoot and branches alike in vigor. Stem lacking paraphyllia, hidden on all sides by interwoven leaf cilia. Rhizoids occasional, in tight bundles, from stem at immediate base of underleaves, the tips often branched. Leaves widely spreading but with lobes arching toward shoot apex, rather closely imbricate, distinctly succubously (almost longitudinally) inserted, the lamina twisted: ventral sector of leaf oriented parallel with substrate, the dorsal sector of leaf

antically assurgent and the dorsal margin seen on edge, the leaves obtrapezoidal to subreniform, 1250–1650 μm wide × 880–1130 μm long, asymmetrically 4–6-lobed, the ventral pair of lobes largest, the dorsal lobe smallest. Lobes caudate, not 3-fid, the ventral pair of lobes 4–5 cells wide at base (tier immediately above sinus base), then 2–3 tiers of laterally juxtaposed cells basal to the uniseriate row of 6–10 cells; cells of uniseriate row ± cylindrical, with dilated septa, 13–25 μm wide, 62–98 μm long, the cells toward base of uniseriate row rather thick-walled, the cells becoming progressively smaller and less thick-walled toward lobe apices, the surface of penultimate and terminal cells striolate-papillose, that of the remaining cells finely striolate; terminal cell of uniseriate row somewhat tapered, 10–12 μm wide, 68–90 μm long, slightly thick-walled in the tip; margins of lobes copiously armed with pairs of opposing cilia, the cilia of lobes and sinus bases repeatedly dichotomously branched, the branches of each dichotomy stiffly diverging, but the armature primarily directed adaxially and oriented at right angles to the leaf plane, the leaf thus appearing to have a stiffly ciliate adaxial leaf surface, the cilia ultimately forming a densely interwoven dendroid crown to the leaf; marginal cilia of lobe uniformly uniseriate throughout, the cells elongate, rather thick-walled, the surface of cells toward base of cilium striolate, the surface of cells toward and including terminal cell striolate-papillose; sinus bases plane and not reflexed. Disc slightly convex, asymmetric, 3–4 cells high at dorsal sinus, 5–6 cells high at ventral sinus (from base to sinuses); margins of disc with dichotomously branched cilia similar to those of lobes, the cilia often adaxially displaced and lying at right angles to the disc plane. Cells of disc thin-walled, strongly elongated, aligned in somewhat irregular tiers, in lamina middle 22–26 μm wide, 84–108 μm long; surface markedly long-striolate, with only a few papillae. Underleaves somewhat smaller than leaves, narrowly connate on both sides, cuneate, quadrifid, the marginal armature similar to leaves and likewise forming a mass of interwoven cilia; disc 3–4 cells high. Asexual reproduction lacking.

Dioecious. Androecia intercalary on main shoot, notably inconspicuous, the bracts in ca. 3 pairs, of similar size to leaves, transversely inserted at dorsal end, moderately ventricose in basal sector, the dorsal margin somewhat dilated and inflexed, the disc a little higher than leaves (6 cells high at dorsal sinus), the bracts otherwise as in leaves; antheridia large for bract size, 1 per bract, the stalk biseriate. Gynoecia isophyllous, terminal on main shoot, sporadically on long *Frullania*-type branches, subfloral innovations lacking; stem perigynium present, 2(3)-stratose, obscurely and bluntly trigonous, with 3 series of bracts and bracteoles inserted on it, the bracts and bracteoles with their laminae erect, clasping the perianth and closely adhering to its contours but with the lobes moderately spreading, each series ensheathing the perianth, the lateral margins mutually connivent but free from one another; bracts and bracteoles similar in size and form, deeply convex (dorsal view), those of first and second series subequal in size, those of innermost series similar to bracts and bracteoles of series immediately below (second series) except for the slightly smaller size, the less armed lobe bases and the greater number of simple cilia of the lamina margins, the bracts and bracteoles of innermost series symmetrically narrowly ovate, 3–4-lobed to 0.35–0.45, the lobes long-ciliiform, terminating in a uniseriate row of 7–11 elongated, thick-walled cells with slightly swollen septa, the lobe bases entire or with 1–2 pairs of opposing simple or branched cilia, the lamina distinctly inflated at base, the margins with simple (or somewhat less common) once-forked cilia, the 2 cilia of "fork" subequal. Perianth present and well developed, the transition from stem perigynium to perianth not evident in either external or internal aspect, the outer surface of the entire sporophyte protective device (stem perigynium + perianth) densely invested with short, simple or branched hairs (the inner face of the perianth with a few hairs distally, smooth

in median and basal sectors), the perianth rather sharply trigonous distally (the third keel ventral), the intervening sulci deep, the perianth tapered toward mouth, the mouth not or at most feebly contracted, fringed with stiff cilia, the cilia comprised of 2–4 elongated (to 9:1) thick-walled cells with a distinctly papillose surface, the tip cell tapering to a rather sharp summit; perianth unistratose (or locally bistratose) in distal and median sectors. Shoot calyptra apparently lacking, the unfertilized archegonia at or near calyptra base (gynoecia seen only in a state soon after fertilization).

Sporophyte unknown.

Type: *Castanoclobos julaceus* (Hatcher *ex* J.J.Engel) J.J.Engel & Glenny (≡ *Leiomitra julacea* Hatcher *ex* J.J.Engel)

A monotypic genus with only *C. julaceus*, endemic to New Zealand. Engel and Glenny (2007) removed the species from *Leiomitra* and established a new genus for it based upon presence of a well-developed perianth, trigonous and ciliate at the mouth, and brown pigmentation.

References: Engel (1999b); Engel and Glenny (2007).

Castanoclobos julaceus (Hatcher *ex* J.J.Engel) J.J.Engel & Glenny

[Plate 3D, E; Figs. 22, 22A]

Leiomitra julacea Hatcher *ex* J.J.Engel, Novon 9: 26. *f. 1.* 1999. *Trichocolea julacea* Hatcher, Trans. Roy. Soc. New Zealand 85: 245. *f. 30–36*. 1958, *nom. inval.* (Art. 37). *Castanoclobos julaceus* (Hatcher *ex* J.J.Engel) J.J.Engel & Glenny, Novon 17: 425. 2007. Holotype: New Zealand, Stewart Is., Port Pegasus, Sawmiller's Arm, 1949, *Martin 621* (F); isotypes: (CHR, UWM).

The generic description serves to characterize the single species.

Distribution and Ecology: Endemic to New Zealand. Known only from the type collection, two specimens from South Cape on Stewart Island, from the Cascade ultramafic moraine in southern Westland and on the nearby Teer Plateau. At the Cascade, the species occurs at ca. 135 m in an area of ultramafic rocks and outcrops with rather open vegetation consisting of mainly of *Gleichenia*, *Lycopodium*, *Juncus*, the lichen *Cladonia* and scattered *Leptospermum scoparium*. The species forms thick, nearly pure mats on well-drained soil of slopes and vertical banks of drainage channels. On the Teer Plateau, it was found under short *Leptospermum scoparium*, *Halocarpus biformis* and *Lepidothamnus intermedius* forest at 340 m, with *Acromastigum anisostomum* and *Geocalyx caledonicus*. One of the South Cape sites is at 200 m, in wind-swept prostrate *Leptospermum scoparium* shrubland up to 80 cm high, with *Gahnia procera* and *Dracophyllum longifolium*, on peat, with *Acromastigum anisostomum*, *Adelanthus occlusus*, *Anastrophyllum schismoides* and *Campylopus clavatus*. A second, nearby site had *Dracophyllum longifolium*, *Lepidothamnus intermedius*, *Leptospermum scoparium* and *Olearia colensoi* scrub 1.5–2.5 m high, and the plants were on peat with *Adelanthus occlusus*, *Lepidozia ulothrix*, *Leptoscyphus australis* and *Marsupidium surculosum*. At the type locality, the vegetation included *Nothofagus solandri*, and perhaps *Lepidothamnus intermedius*. Accompanying species were *Cladia aggregata*, *Cladina confusa*, *Jamesoniella colorata*, *Plagiochila baileyana*, *Radula dentifolia* and *Telaranea herzogii*. Hatcher (1958) mentions that the type was "epiphytic; on forest trees" but the presence in the type collection of leaf litter and *Plagiochila baileyana* makes this doubtful.

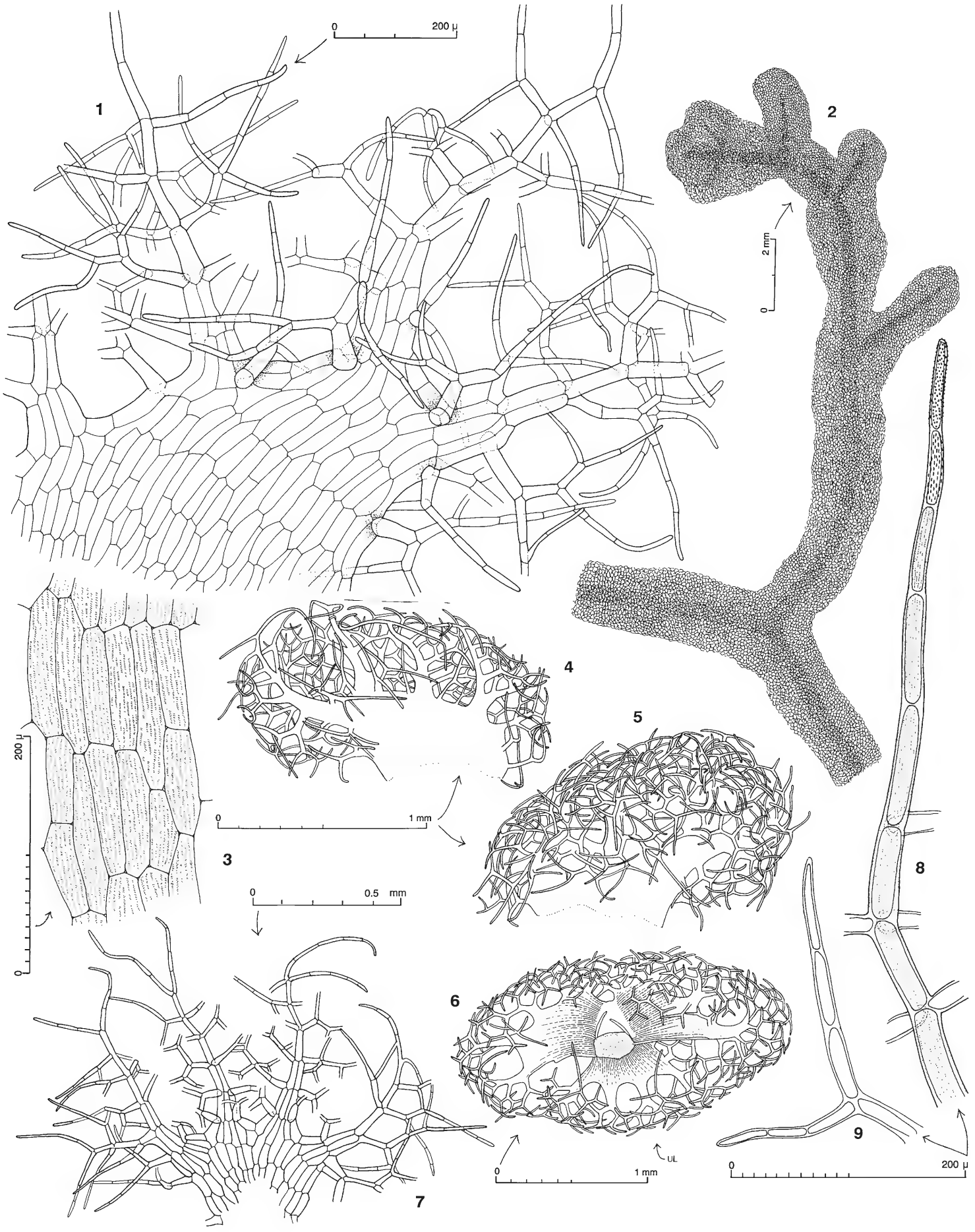

Fig. 22.
Castanoclobos julaceus (Hatcher *ex* J.J.Engel) J.J.Engel & Glenny. 1. Ventral sector of leaf, adaxial aspect (some portions of marginal armature not shown for clarity). 2. Shoot, dorsal view. 3. Median cells of lamina. 4. Leaf, adaxial view. 5. Leaf, abaxial view. 6. Cross section of shoot showing mass of interwoven, branched cilia (UL = underleaf) of one gyre. 7. Underleaf (some portions of marginal armature not shown for clarity). 8. Leaf lobe, distal sector. 9. Lateral armature of leaf lobe, distal sector. (All from holotype.)

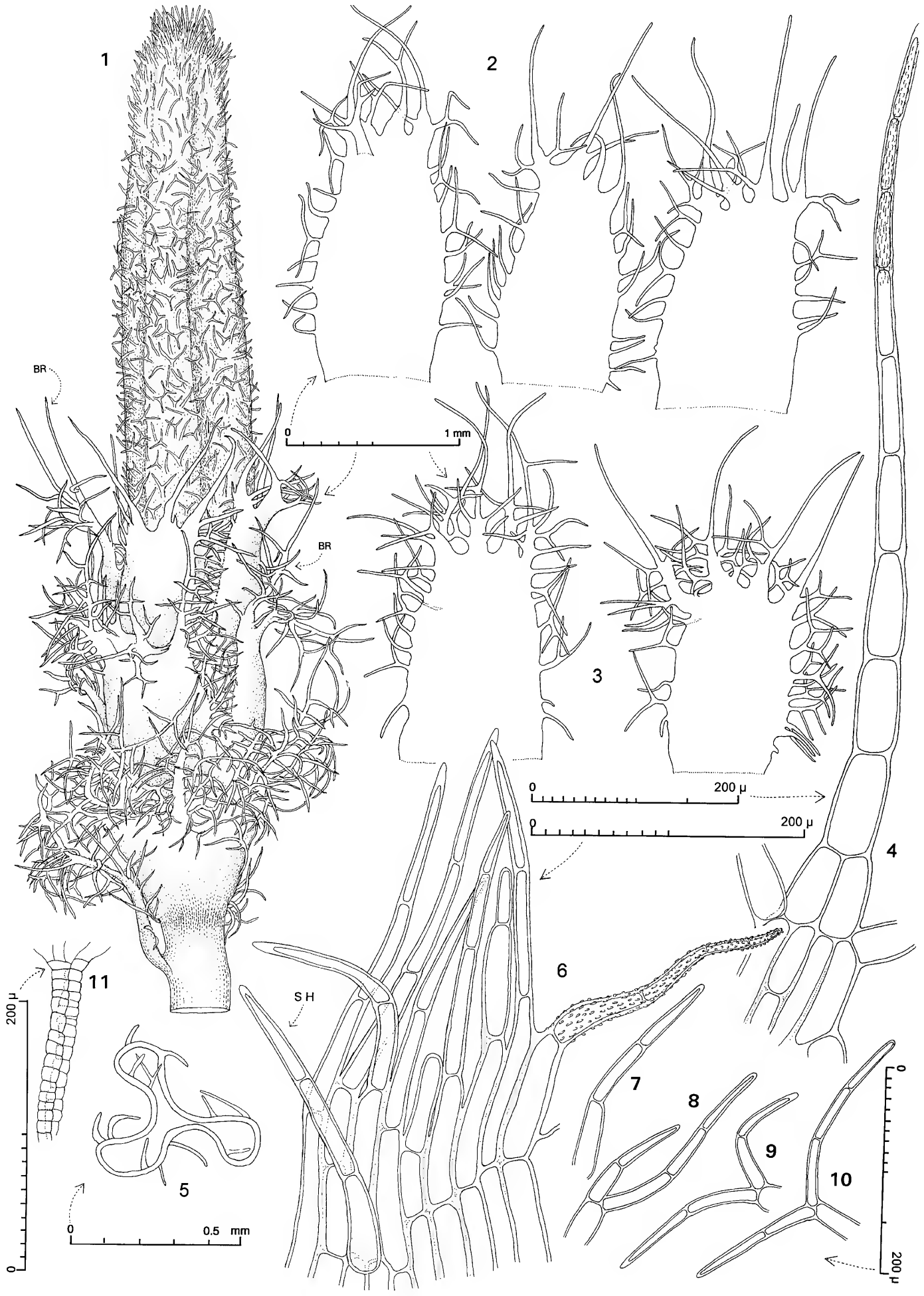

Fig. 22A.

Castanoclobos julaceus (Hatcher *ex* J.J. Engel) J.J.Engel & Glenny. 1. Gynoecium, ventral view (BR = bract); note ± isophyllous condition. 2. Innermost bracts, and in middle, bracteole. 3. Bracteole (left) and bract from second series. 4. Lobe of innermost ♀ bract, the surface striolae shown in part. 5. Perianth, cross section through distal portion. 6. Portion of perianth mouth with surface papillae shown in part (SH = surface hair). 7–10. Hairs of perianth surface. 11. Antheridial stalk. (All from *Y. Qiu & Braggins NZ-03128*, New Zealand, South Is., Westland, 19 km on Jackson River Rd. from Arawata River Bridge, ultramafic site.)

Comments: The species, known for many years only sterile, initially was described as a *Trichocolea* by Hatcher (1958) and transferred to *Leiomitra* by Engel (1999b). Engel and Glenny (2007) demonstrated that the gynoecium of *Castanoclobos julaceus* is quite different from that of *Leiomitra*. In *Leiomitra* the bracts and bracteole of the innermost series are well developed and either free and then a perianth entirely lacking, or fused to form a low, vestigial perianth (e.g., *L. lanata*, Fig. 23: 2). *Castanoclobos*, on the other hand, has a well-developed perianth that is rather sharply trigonous distally (Fig. 22A: 5, cross section) and has a ciliate mouth (Fig. 22A: 6). The perianth is subtended by a stem perigynium with three cycles of bracts and bracteoles inserted on it (Fig. 22A: 1). In *Castanoclobos* the surface of the entire sporophyte protective device (stem perigynium + perianth) is densely covered with short, simple or branched hairs (Fig. 22A: 1, 7–10) vs. a smooth coelocaule surface in *Leiomitra*.

Engel and Glenny (2007) retained *Castanoclobos* in the *Trichocoleaceae* because of the distinct presence of a trichocoleoid gametophyte architecture, especially the form of the leaf lobes with branched cilia, and the complete lack of ventral-intercalary branching; both of these characters are absent from the *Pseudolepicoleaceae*, where some might argue that it may belong. Molecular studies perhaps may prove useful in establishing the systematic affinities of *Castanoclobos*.

The leaves of this species are remarkable for their development of a densely interwoven "basket-work" of cilia (Fig. 22: 4–6), which causes the axis and branches to appear spongy and julaceous (Fig. 22: 2); the cilia are repeatedly dichotomously branched and widely divergent, the ultimate divisions of each leaf forming a densely interwoven dendroid "crown." Branching is irregularly sympodial to pseudodichotomous, as in *Leiomitra lanata* (see Figs. 22: 2; 23: 1), but the form of the leaves is very different in the two species. In *L. lanata* leaf lobes are equally 3-fid, consisting of an adaxially divergent segment and a pair of abaxially divergent segments, each segment usually 1(2) times again 3-fid, ending in a pair of ± equally divergent, uniseriate cilia. In *C. julaceus*, on the other hand, leaf lobes are not 3-fid, but rather simply caudate, with margins armed with pairs of opposing cilia (Fig. 22: 1). The cilia are repeatedly dichotomously branched and form a densely interwoven dendroid crown (Fig. 22: 1, 4, 5).

The species is readily distinguished in the field by the julaceous, wiry aspect of the plants coupled with the brownish color.

Leiomitra Lindb.

Leiomitra Lindb., Acta Soc. Sci. Fennica 10: 515. 1875. *Trichocolea* subg. *Leiomitra* (Lindb.) Spruce, J. Linn. Soc., Bot. 30: 353. 1895.
Basichiton Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 394. 1877.
Trichocolea sect. *Cryptocaulia* Hatcher *ex* R.M.Schust., Nova Hedwigia 15: 446. 1968. *Trichocolea* sect. *Cryptocaulia* Hatcher, Lloydia 22: 213. 1959, *sin. descr. lat.*

Plants soft-textured, felt-like, loosely prostrate, pale green to yellowish green to pure green, moderately large. Branching relatively sparing, usually irregular and monopodial and with branches soon similar in vigor to primary axis or (subg. *Brachygyna*) ± pinnate; branching (ours) all of the *Frullania* type; *Acromastigum*-type branches at times sparingly present in subg. *Brachygyna*. Stem paraphyllia present in some species, smooth in others, lacking differentiation of a cortex, the cortical cells thin-walled. Leaves *Trichocolea*-like in aspect, appearing as a mass of uniseriate, filamentous, interwoven cilia, the insertion succubous, 4-lobed, but becoming 5–8-lobed with secondary subdivision, the lobes asymmetric, the ventral 2–3

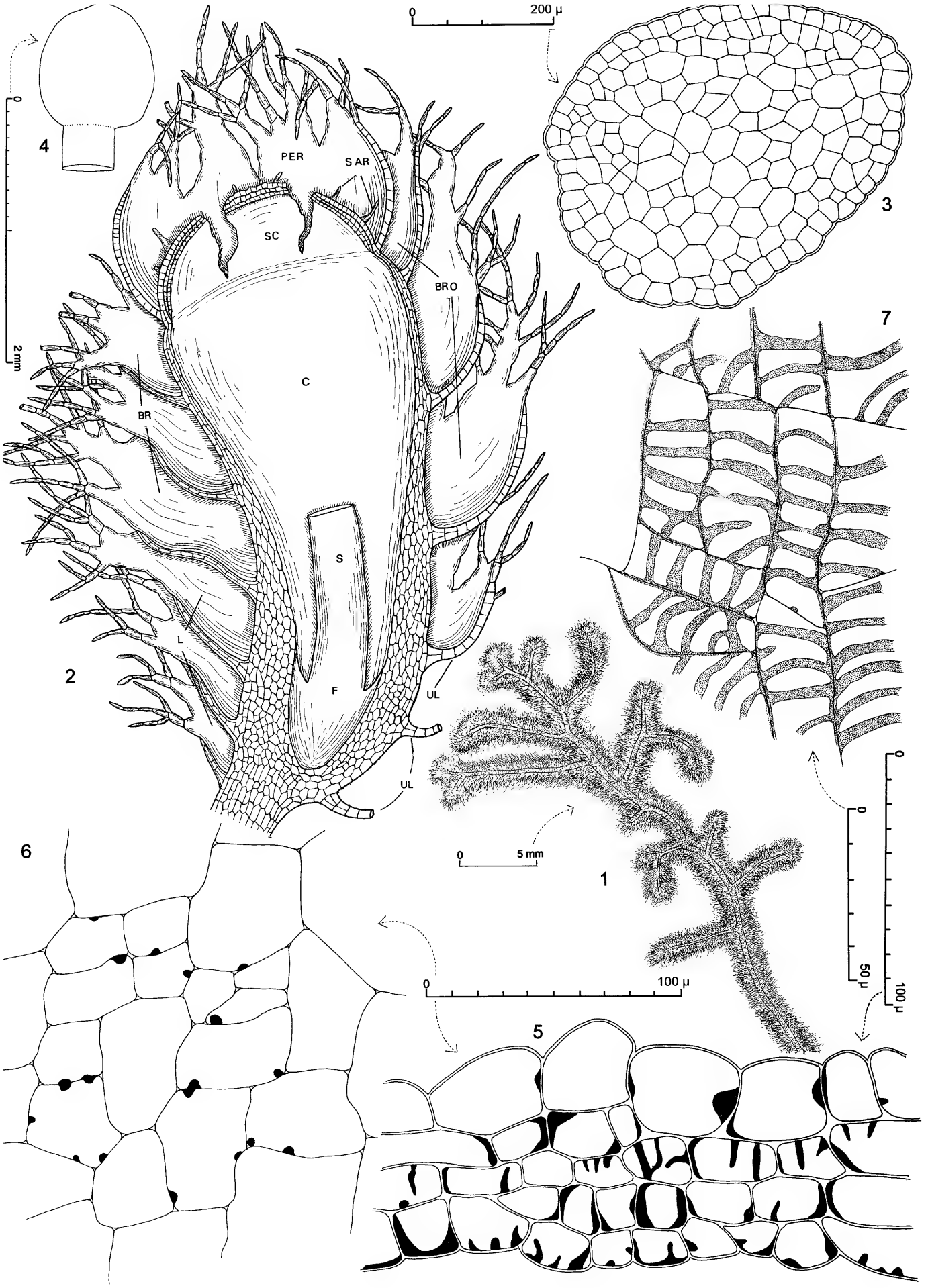

Fig. 23.
Leiomitra lanata (Hook.) R.M.Schust. 1. Plant showing distantly and irregularly 1-pinnate branching, dorsal view (note secondary branches are few and no more than one per primary branch). 2. Mature? inflorescence, median longitudinal section (C = coelocaule; SC = shoot calyptra; SAR = sterile archegonia; PER = perianth; BR = bracts; BRO = bracteoles; L = leaves; UL = underleaves; S = seta; F = foot). 3. Seta, cross section. 4. Capsule profile. 5. Capsule wall, cross section. 6. Capsule wall, outer layer. 7. Capsule wall, inner layer. (Fig. 1, 3–7, from *Engel 17761*, New Zealand, South Is., Otago, Morrisons Creek; 2, after Hatcher, 1959.)

lobes larger than the dorsal, the lobes mostly 2–3-furcate, with each subdivision fringed with opposed, paired, uniseriate, elongated, tapered cilia that are mostly 3–7(8) cells long; disc low, formed of imperfectly rectangular, often ± tiered cells. Surface cilia and disc ± papillose above to striate-papillose proximally. Underleaves deeply bifid, the primary lobes often again bilobed (the underleaf then bisbifid); lobes armed as in leaves. No asexual reproduction.

Dioecious. Androecia terminal but eventually intercalary; bracts few, leaf-like; antheridia 1–2 per bract, the stalk biseriate. Gynoecia terminal on leading shoots (in subg. *Brachygyna* on short lateral branches), typically with 1–2 subfloral innovations, the innovations long and sterile or short and ♀. Coelocaule usually abbreviated, lacking surface paraphyllia, the bracts and bracteoles of first and second series inserted on the coelocaule, those of innermost series well developed, free (and then a true perianth completely lacking) or fused to form a low, vestigial perianth; calyptra present, free, smooth, globose to ovoid-globose, with unfertilized archegonia at or near the base (true calyptra) or scattered on at least the basal half (shoot-calyptra developed), the distal portion of sporophyte protected by the calyptra + bracts and/or a perianth.

Seta short. Capsule spherical to short-ellipsoidal (the length:width ratio less than 1.2:1), the wall (4)5–6-layered, the outer layer of cells hyaline, large, with small knot-like thickenings or the cells altogether devoid of thickenings; innermost layer of cells with small nodular thickenings, without spurs or semiannular bands.

Spores finely granular or granular asperulate. Elaters bispiral or less often 3-spiral or 2–3-spiral.

Type: *Leiomitra tomentosa* (Sw.) Lindb. (≡ *Jungermannia tomentosa* Sw.)

A genus of ca. 12 species. The majority are tropical: Seven occur in the Neotropics (for species treatments see Hatcher, 1958 and Schuster, 2001d), two are Paleotropical, including *Leiomitra breviseta* (Steph.) R.M.Schust. which ranges from New Guinea to the Solomon Islands and the Philippines (see Piippo, 1984). Two species are present in southern South America, *L. elegans* (Lehm.) Hässel (also in Juan Fernandez) and *L. smaragdina* Hässel (see Hässel [2002] and also comments in Engel [1978]). A single species, *L. lanata*, occurs in New Zealand. *Leiomitra julacea* was placed in *Castanoclobos* by Engel and Glenny (2007).

Leiomitra differs from *Trichocolea* in having a very different branching pattern: irregular, sparing and monopodial, with the branches soon becoming similar in vigor to the main, leading shoot (Fig. 23: 1), but also in a) presence of a low but distinct calyptra (Fig. 23: 2); b) presence of at least a reduced but perceptible perianth (Fig. 23: 2); and c) the spherical capsule (Fig. 23: 4).

References: Hatcher (1958; rev.); Stewart (1978; oil-bodies of *Leiomitra lanata*); Taylor and Hollensen (1970; ♀ inflorescence of *L. lanata*); Schuster (2000a, 2001d).

Key to Species

1a. Leaf lobes equally 3-fid, consisting of an adaxially divergent segment and a pair of abaxially divergent segments, each segment usually 1(2) times again 3-fid, ending in a pair of ± equally divergent, uniseriate cilia; leaf disc 6–10 cells high. Common, North and South Is. . . . . *L. lanata* (p. 176)

1b. Leaf lobes caudate, not 3-fid, the margins armed with pairs of opposing cilia, the cilia repeatedly dichotomously branched and forming a densely interwoven dendroid crown; leaf disc 5–6 cells high. Rare, Stewart Is. and Westland only . . . . . [*Castanoclobos julaceus*, p. 170]

Leiomitra lanata (Hook.) R.M.Schust.

[Plate 3F; Fig. 23; Fig. 24: 2, oil-bodies, p. 178]

Jungermannia lanata Hook., Musci Exot. 2: *pl. 116*. 1819. *Trichocolea lanata* (Hook.) Nees, Naturgesch. Eur. Leberm. 3: 116. 1838. *Leiomitra lanata* (Hook.) R.M.Schust., Phytologia 45: 417. 1980. Type: New Zealand, South Is., Dusky Bay, 1791, *Menzies*.

Plants soft and distinctly woolly in appearance, prostrate, densely interwoven, clear grass green to a little yellowish green in life, dark olive-green in herb., 35–65 mm long, the shoots 1.8–3.8 mm wide, with apices somewhat swollen. Branching irregularly sympodial to pseudodichotomous (or less often distantly and irregularly 1-pinnate), the leading axis soon losing its dominance, the main shoot and branches alike in vigor, the longest branches 8–12 mm long. Stems flexuous, lacking paraphyllia. Rhizoids rather common, from stem at immediate base of underleaves, the tips often branched. Leaves widely spreading, the lobes and cilia oriented in ± the same direction as disc, the leaves closely imbricate, the insertion and orientation strongly succubous, suborbicular to subreniform, 2250–2900 μm wide × 1750–2250 μm long, divided into 5–7 non-pinnulate lobes (the lobes in ventral sector of leaf larger), each lobe ± equally 3-fid from near the base and consisting of an adaxially divergent segment and a pair of abaxially divergent segments, each segment 2–3 cells wide at base and usually 1(2) times again 3-fid, ending in ± equally divergent cilia, the ultimate cilia uniseriate throughout. Lobes caudate, the ventral 7–10 cells wide at base, the ultimate cilia tapering toward tip, the cells rather thick-walled, the septa ± thickened and dilated, the surface with fine, short striolae and papillae, the penultimate cell 14–19 μm wide, (120)130–168(186) μm long; terminal cell tapering to a sharp, often apiculate point, (7)9–12 μm wide, 108–144 μm long, thick-walled in the tip, the surface as in cells below; sinus bases plane and not reflexed, normally lacking armature. Disc clearly evident, asymmetric, 6–10 cells high (from base to highest sinuses which are in median-ventral sector of leaf), the disc lowest in vicinity of dorsal sinus base; margins of disc 1–2 ciliate or entire. Cells of disc distinctly thin-walled, in lamina middle 30–35(43) μm wide × 93–138(150) μm long; surface finely striate-papillose. Oil-bodies markedly small for cell size, hyaline and somewhat glistening, 6–16(20) per cell in median sector of disc, up to 33 per cell in cilia, finely papillose, the spherules distinctly projecting beyond membrane, subglobose to elliptic (often irregularly so), 3.4–3.8 × 6.2–8.2 μm, spherical ones 4.8–6.7 μm in diam. Underleaves *in situ* appearing as a mass of cilia, much smaller than leaves, narrowly connate on both sides (on one side often obscurely so by a long narrow strip), reniform, 4–6-lobed, each lobe with same basic repeated 3-fid architecture as leaves except the basal-most 3-lobed unit obscurely in two planes or in one plane, the ultimate cilia similar to those of leaves; disc 1–3 cells high. Asexual reproduction lacking. Fungal partner absent.

Androecia intercalary on main shoot or short to long branches, the bracts often somewhat smaller than leaves, transversely inserted at dorsal end, distinctly ventricose in dorsal-basal sector, the free margin of ventricose sector with simple or bifid cilia, the abaxial face of

swollen sector smooth, the bracts otherwise as in leaves; antheridia large for bract size, 1–2 per bract, the stalk biseriate. Gynoecia on main shoot or leading branches, but becoming axillary or pseudolateral (through development, respectively, of 2 or 1 subfloral branches); coelocaule low, stoutly clavate, thick and fleshy below but becoming thin and ± membranous at the cap-like summit, with 4 series of bracts and bracteoles inserted on it, the bracts similar to leaves except ± symmetrical and transversely inserted, the bracteoles slightly smaller than bracts, otherwise similar to underleaves; shoot-calyptra present. Perianth rudimentary, consisting of a ring of lobed, irregularly shaped, sometimes ± plicate bracts + bracteole that range from completely free except for a low fusion on one side of bracteole to fusion of all members, the union always low, at times barely discernible.

Seta massive, 0.85 mm and 16–18 cells in diam., up to 32 mm long, with numerous (ca. 65) rows of outer, smaller cells, the internal cells gradually becoming larger toward seta middle. Capsule almost spherical, ca. 1.3–1.5 mm wide × 1.6–1.8 mm long, feebly beaked at the tip, irregularly dehiscing or dehiscing into 4 equal valves, the walls brittle, 62–79 μm thick, of 4–6 layers; outer layer of cells small, irregularly quadrate to short-rectangular, thin-walled, delicate, hyaline, with minute, knot-like thickenings on longitudinal and/or transverse walls or the cells altogether devoid of thickenings; innermost layer of cells of very irregularly oriented, various-sized cells, the radial walls with somewhat thick continuous sheets of red-brown material, with semiannular bands common, rather narrow, usually complete, rarely forked.

Spores 11.5–13 μm in diam., with low but sharply defined, close papillae and short-vermiculate markings. Elaters somewhat contorted, bluntly pointed at the ends, short, 10.1–11 μm wide, bispiral to the tips, the spirals 2.9 μm wide.

Distribution and Ecology: Endemic to New Zealand and a rather common species in rich, damp forests of Stewart Is. (0–70 m) as well as both South Island (0–460 m) and North Island (0–700 m). Known from Rakiura (Stewart Island, Solander Island), Fiordland, Southland (Bluff Hill), Otago (Otago Coast ER), Westland, Western Nelson, Southern North Island, Volcanic Plateau, Gisborne (Urewera), Auckland (west coast and Coromandel) and Northland EPs.

The species occurs in lowland tall forest, mostly of mixed podocarps (*Dacrydium*, *Dacrycarpus*, *Podocarpus* and *Prumnopitys*), *Weinmannia* and *Nothofagus* on the forest floor, rotted logs, rotted, often decorticated wood on the floor, bedrock, and in such niches it may be locally abundant and form large, pure mats. It sporadically occurs on the lower sectors of tree trunks and exposed roots. It is rarely epiphytic on tree trunks or tree-fern trunks. Accompanying species are *Achrophyllum quadrifarium*, *Aneura alterniloba*, *Balantiopsis diplophylla*, *Categonium nitens*, *Cyathophorum bulbosum*, *Distichophyllum pulchellum*, *Heteroscyphus coalitis*, *Hymenophyton flabellatum*, *Metzgeria leptoneura*, *Nertera villosa*, *Plagiochila baileyana*, *Psiloclada clandestina*, *Ptychomnion aciculare*, *Pyrrhobryum bifarium*, *P. mnioides*, *Schistochila balfouriana*, *S. glaucescens*, *S. nobilis*, *Temnoma pulchellum*, *Thuidium furfurosum*, *Trichocolea hatcheri*, *T. mollissima*, *Tylimanthus saccatus* and *Weymouthia cochlearifolia*.

Comments: The leaves of *Leiomitra lanata* and *Castanoclobos julaceus* appear superficially similar but actually are strikingly different. In *C. julaceus* the cilia are repeatedly dichotomously branched and stiffly diverging, the ultimate ramifications of the cilia forming a densely interwoven "surface" that lends the plant a compact, julaceous appearance, as compared with the more loosely wooly aspect of *L. lanata*. The leaves of *L. lanata* are relatively simple by comparison, with lobes equally 3-fid from near the base, and the cilia rather straight and equally spreading in all directions.

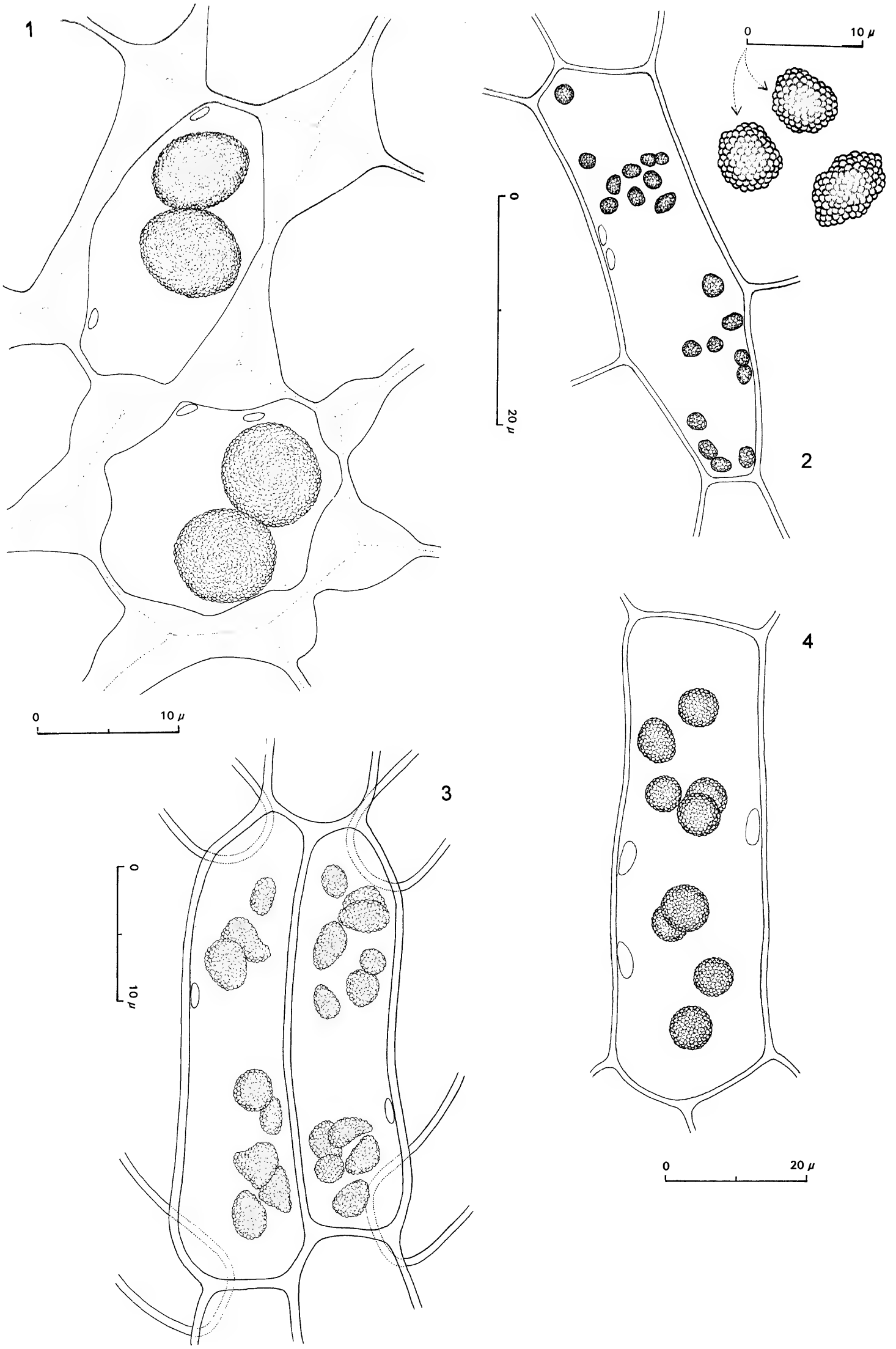

Fig. 24.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Archeophylla schusteri* (E.A.Hodgs. & Allison) R.M.Schust. Disc cells. 2. *Leiomitra lanata* (Hook.) R.M.Schust. Disc

Most similar in appearance to *Temnoma pulchellum*, as both are highly ciliate and are found in similar habitats, occasionally together. In *Leiomitra lanata*, the leaf disc is obscured by the cilia, whereas in *T. pulchellum* it is easily visible.

Trichocolea Dumort.

Trichocolea Dumort., Commentat. Bot. 113. 1822, corr. Nees, Naturgesch. Eur. Leberm. 3: 101, 103. 1838, *orthogr. cons.*

Plants loosely procumbent, less often creeping or pendulous, pale yellowish to whitish green, becoming almost whitish when dry, typically vigorous. Branching usually (1)2–3(4)-pinnate, the branches all of *Frullania* type, never becoming flagelliform and microphyllous. Stems rather fleshy, often paraphyllose, the cortex ill-defined, somewhat smaller than the thin-walled medullary cells. Rhizoids rare or lacking, restricted to underleaf bases. Leaves contiguous to loosely imbricate, usually distinctly succubous, asymmetric, the dorsal lobe(s) somewhat smaller and the dorsal sector of disc somewhat lower, usually obtrapezoidal to subreniform in outline, deeply (3)4-lobed, the principal lobes usually with numerous secondary, smaller lobes, the lobes ultimately becoming resolved into a cobwebby mass of tapered cilia; cilia uniseriate, formed of strongly elongated cells, opposed or verticillate in groups of three; disc on one or both margins often with an accessory lobe or lobes. Cells often at least locally tiered, everywhere narrow and rectangular, those of disc thin- to weakly firm-walled and with trigones absent, those of cilia longer; surface of lobes papillose-striolate, becoming striolate toward disc base. Oil-bodies small, ranging up to 15(20), finely granular to irregularly granular-papillose. Underleaves somewhat smaller than leaves, symmetrical, bifid, the lobes again bifid and the underleaves then bisbifid, or (*T. rigida*) quadrilobed, the margins armed as in leaves. No asexual reproduction.

Dioecious. ♂ Branches similar to vegetative branches; bracts in 12–15 or more pairs, leaf-like except the disc concave and higher and the lobes shorter; antheridia 1–2 per bract. Gynoecia terminal on main shoots (but often secondarily displaced to one side because of vigorous growth of a subgynoecial branch); bracts and bracteoles inserted at or below coelocaule base, similar to leaves and underleaves except larger and more copiously lobed and ciliate; bracteoles like underleaves, but larger. Coelocaule prominent, developing with fertilization, clavate to obpyriform, the wall polystratose, hispid in appearance, covered by ± reduced bractlets and variable paraphyllia, a perianth lacking; calyptra absent, the unfertilized archegonia remaining hidden among the mass of paraphyllia at coelocaule summit, the developing sporophyte deeply boring into shoot apex and protected entirely by stem tissue (i.e., the coelocaule).

Seta long, massive, often hollow with maturity. Capsule ellipsoidal (the length:width ratio 2–2.5:1), the wall (5)6–8-layered, the outer layer of cells large, hyaline, usually lacking

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cells, at right 3 oil-bodies at higher magnification. 3. *Trichocolea rigida* R.M.Schust. Paired cells at lobe base. 4. *Eotrichocolea polyacantha* (Hook.f. & Taylor) R.M.Schust. Cell at base of uniseriate row. (Fig. 1, from *Glenny 9282*, New Zealand, South Is., Western Nelson EP, Sewell Peak; 2, from *Glenny 9012*, New Zealand, South Is., Westland EP, Big Wainihinihi R.; 3, from *Glenny 9601*, New Zealand, South Is., Western Nelson EP, Stockton Plateau; 4, from *Glenny 9114*, New Zealand, South Is., Westland EP, Mt. Brown.)

pigmented wall-thickenings; innermost layer of cells with nodular to spine-like thickenings that often extend across the free tangential walls as complete semiannular bands.

Spores granular, 1.3–2× elaters in diam. Elaters bispiral.

Type: *Trichocolea tomentella* (Ehrh.) Dumort. (≡ *Jungermannia tomentella* Ehrh.)

A genus of ca. 20 species, most of which are tropical montane. Six are Neotropical, and six are Paleotropical in distribution; New Guinea has three species: *Trichocolea fragillima* Herzog, *T. gracillima* Austin and *T. pluma* (Reinw., Blume & Nees) Mont. The last has the broadest distribution, ranging from New Guinea to the Philippines to Asia. While the Neotropical species were revised by Hatcher (1959), the Paleotropical taxa await taxonomic study. One species, *T. tomentella* (Ehrh.) Dumort., is basically suboceanic–oceanic over a broad range in temperate areas of the Northern Hemisphere. Three species occur in New Zealand, and, interestingly, the only southern temperate members of the genus are Australasian. The southern South American *T. elegans* Lehm. has been transferred to *Leiomitra* by Hässel (2002).

References: Hatcher (1958; rev.); Stewart (1978; oil-bodies of *T. mollissima*); Taylor and Hollensen (1970; studies of ♀ inflorescences); Schuster (1968b, 2000a, 2001d).

Key to Species

1a. Cilia of leaves strongly tapered, the cells in cilia with dilated septa; terminal cell of lobes weakly to strongly tapered, ca. 8–10 × 120–170 μm, thick-walled, almost smooth or delicately striolate, ending in sharp, thick-walled points or (*T. hatcheri*) a ± rounded tip; dry plants glistening 2

2a. Plants robust, ascending or when arboreal, pendulous, usually regularly 3-pinnate (♂ plants often only 2-pinnate); disc of stem leaves 3–5 cells high; terminal cell of leaf lobes tapering to a sharp point, the tip usually thick-walled; stem paraphyllia abundant. Widespread throughout New Zealand . . . . . *T. mollissima* (p. 183)

2b. Plants small, closely prostrate to adnate, regularly, closely 2(3)-pinnate, pinnae of third order rare; disc of stem leaves 2–3 cells high; terminal cell of leaf lobes tapering to a ± rounded tip, the tip thin-walled; stem paraphyllia few or altogether absent. Occurring sporadically on Stewart Is., South Is. and North Is. . . . . *T. hatcheri* (p. 188)

1b. Cilia of leaves formed of cylindrical cells that are hardly tapered, the cells in cilia constricted at the septa; terminal cell of lobes finger-like and with ± parallel sides, ca. 12–14 × 55–60 μm (ca. 4–5:1), thin-walled, sharply papillose, not thickened at the tip; dry plants dull, more rigid, usually 1 to 1–2-pinnate . . . . . *T. rigida* (p. 180)

Trichocolea rigida R.M.Schust.

[Fig. 24: 3, oil-bodies, p. 178; Fig. 25]

Trichocolea rigida R.M.Schust., Nova Hedwigia 15: 447. *f. 50: 1–7.* 1968. Holotype: New Zealand, South Is., Otago Prov., Old Man Ra., ca. 4000 ft., *Schuster 67-523* (herb. Schuster); isotypes: (herb. Grolle, NICH, OTA, S).

Plants relatively rigid, woolly in appearance, prostrate, densely interwoven, yellow-green, whitish with age, the dried plants dull, appearing amorphous and resembling a crustose lichen, the shoots small, to 1 cm wide, including branches. Branching irregularly 2-pinnate, with 2–4(5) ± irregularly curved, secondary branches per primary branch; branches julaceous, with a woolly appearance, with all sides appearing as a mass of interwoven cilia. Stems rather stiff, paraphyllia rather abundant, much branched, with cells similar to those of the leaf cilia. Rhizoids usually absent. Leaves of stem widely spreading but with lobes and cilia broadly arching upward toward shoot apex, the leaf thus somewhat hand-like, the leaves *in situ* appearing as a dense mass of cilia, the individual lobes hardly discernable, the leaves on the stem approximate, becoming imbricate on branches, semiamplexicaul, the insertion transverse to weakly succubous, obtrapezoidal to subreniform, divided into 4–5 erect, pinnulate lobes, the lobes sometimes appearing forked or partially fused at base (those in ventral sector of leaf somewhat larger), each lobe actually unequally and irregularly (2)3-fid, consisting of a stronger, erect, pinnulate division and (0)1–2 small, freely branched and variably positioned accessory divisions that are 1–2(3) cells wide at the base, and stiffly abaxially spreading and arched in same direction as the main lobes, the divisions armed with pairs of opposing branched cilia. Lobes caudate, ± regularly pinnulate (best seen in adaxial view), with numerous stout segments and cilia, the ventral lobes 4–6 cells wide at base, with 3–5 tiers of laterally juxtaposed, turgid cells basal to the uniseriate row of (4)5–7(8) cells; cells of uniseriate row short, barrel-shaped, rather thin-walled and ± turgid, constricted at the septa, the septa not thickened or dilated, the surface coarsely papillose, the penultimate cell (14)17–24 μm wide, (43)50–67(74) μm long; terminal cell of uniseriate row finger-like, slightly tapering to a broadly rounded apex, 12–22 μm wide, 50–65(82) μm long, thin-walled in the tip, the surface distinctly papillose; margins of lobes armed with pairs of abaxially displaced, opposing cilia, the cilia usually branched (often repeatedly so), the armature all inserted on the abaxial surface of lobe and abaxially patent, but ascending and nearly as long as lobes; marginal cilia of lobe mostly uniseriate throughout, the cilia bases rarely with 2 laterally juxtaposed cells, the cells similar to those of the uniseriate sector of leaf lobes; sinus bases plane and not reflexed. Disc weakly asymmetric, consisting of a low, wide strip 3–4 cells high (from base to sinuses); margins of disc with freely branched cilia, the cilia cells similar to those of lobes, the cilia sometimes abaxially displaced and lying at right angles to the disc plane. Cells of disc faintly uniformly thick-walled, in lamina middle 22–34 μm wide, 53–75(80) μm long; surface densely striate-papillose to striolate. Oil-bodies within all cells of leaf including tip cell of cilia, occupying small portion of cell lumen, opaque, smokey grey, 4–8(12) per paired cells at lobe base, irregularly and inconspicuously and finely granular, the spherules tiny and irregular, the oil-bodies irregular in shape: globose to bottle-shaped to elliptic to sublinear to subcrescentic to subsigmoid, 4.3–4.8 × 7.2–8.6 μm to 2.9–4.8 × 9.6–11.5 μm or spherical and 4.8 μm in diam. Underleaves *in situ* appearing as a dense mass of cilia, somewhat smaller than leaves, free, suborbicular to reniform, quadrifid, often weakly bisbifid, the armature similar to leaves; disc 2–3 cells high.

Androecia intercalary on primary and secondary branches, appearing brushed with apically oriented cilia, the bracts divided to ca. 0.4–0.5, the lamina strongly ventricose, the abaxial face of bract with simple or sporadically branched cilia in distal sector, the armature only sporadically on lamina; antheridia large for bract size, 1(2) per bract, the stalk biseriate. Gynoecia and sporophyte not seen.

Distribution and Ecology: New Zealand: Stewart Island (10–30 m), South Island (0–1390 m), North Island (200–1250 m), Chatham Islands (240 m); Australia: Tasmania and Victoria. In

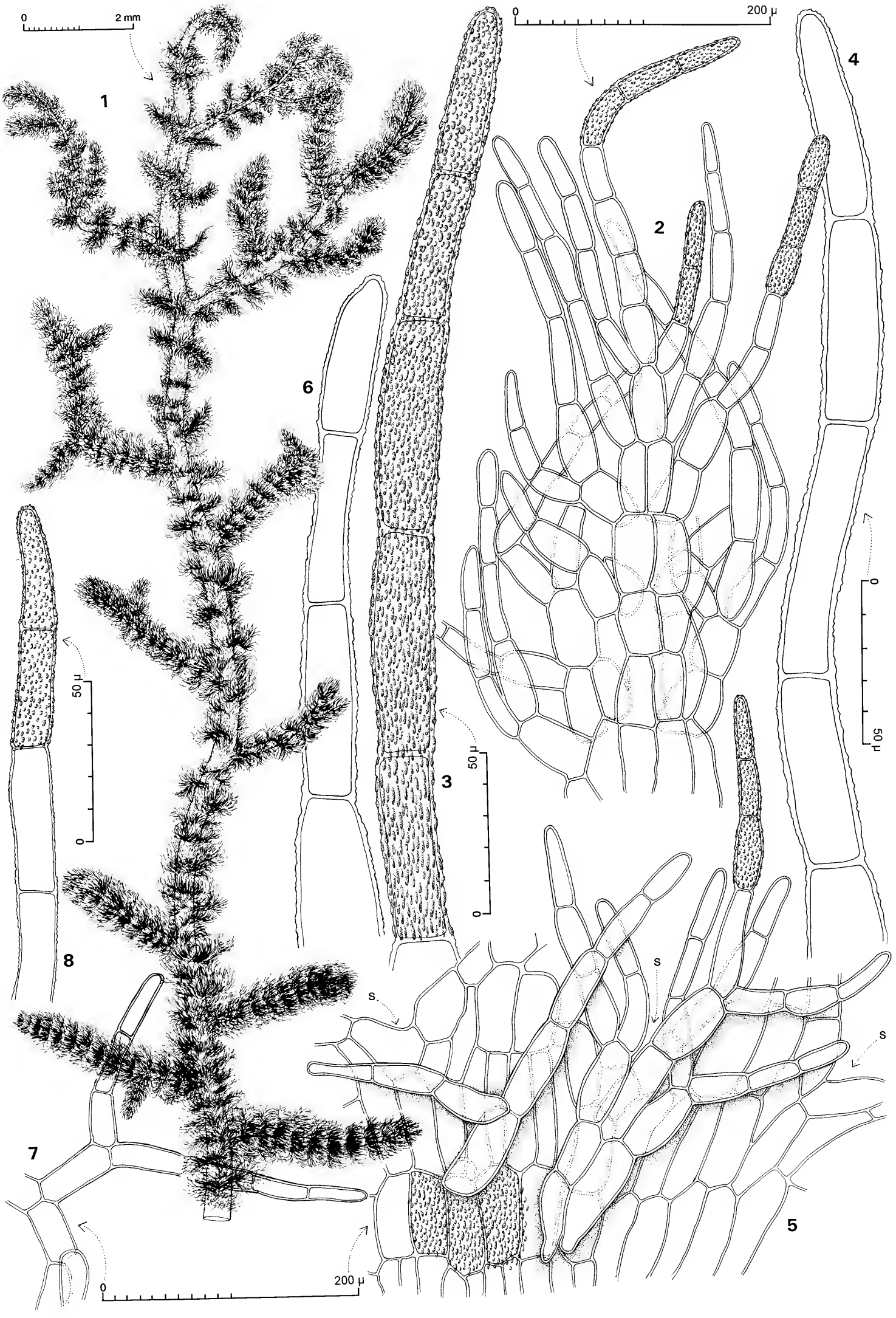

Fig. 25.
Trichocolea rigida R.M.Schust. 1. Plant, dorsal view. 2. Distal portion of leaf lobe (adaxial view, surface detail indicated in part). 3, 4. Apices of leaf lobes, surface detail shown at right. 5. Median

New Zealand known from Northland, Auckland, Volcanic Plateau, Southern North Island (Ruahine and Tararua ranges), Western Nelson (Cobb Valley), Westland, Canterbury (Banks Peninsula, Hawdon River), Otago (Central Otago, Lammerlaw and Otago Coast ERs), Fiordland and Rakiura (Stewart Island, Solander Islands) EPs.

In New Zealand the species is known from scattered localities over a broad altitudinal range. It occurs on the floor and mossy banks in forests near the sea (Martin's Bay and Milford Sound in Fiordland), as well as in upper-elevation forests (e.g., *Nothofagus fusca – N. solandri* var. *cliffortioides* forest at ca. 1280–1390 m at Pinchgut Track, Nelson Lakes Natl. Park). It also occurs in the penalpine zone in damp or springy niches under snow tussock (e.g., in the Lammermoor Ra., Old Man Ra., the type, both in Otago). Also on roadside banks at Halfmoon Bay, Stewart Island. Unlike our two other species, which occur in forests, *Trichocolea rigida* commonly occurs in more open sites, e.g., in seepage areas in penalpine tussock grassland (*Chionochloa*) and exposed roadside banks, and in grassland kept damp by seepage, for instance at Gebbies Pass and Hilltop on Banks Peninsula. At Stockton it occurs under gorse scrub in a gully, on damp soil with adventive grasses and *Polytrichum commune*. On Chatham Island it was found on a soil bank under a canopy of *Dicksonia fibrosa*. Species found with *T. rigida* are *Brachythecium rutabulum*, *Breutelia pendula*, *Chiloscyphus leucophyllus*, *Cratoneuropsis relaxa*, *Distichophyllum pulchellum*, *Drepanocladus aduncus*, *Fissidens asplenioides*, *Canalohypopterygium tamariscinum*, *Plagiomnium novae-zealandiae*, *Pohlia cruda*, *Polytrichadelphus magellanicus*, *Sphagnum australe*, *Thuidium furfurosum* and *Trichocolea mollissima*.

Comments: The species name is in allusion to the more rigid plants, as compared to *Trichocolea mollissima* and *T. hatcheri*. Plants are mostly 1-pinnate, often relatively laxly so vs. the much denser 2-, 2–3-, or 3-pinnate branching of our other taxa. *Trichocolea rigida* is, also, a smaller species, with main axes mostly only 2–4 cm long; when dry it is a relatively dull plant, due to the conspicuously papillose surface, even terminal cells of cilia being clearly roughened (Fig. 25: 3, 5). The cilia are much less strongly tapered, with terminal cells ca. 4–5(5.5)× as long as in basal diam.; the septa between cells are never distinctly dilated (Fig. 25: 1, 3–5). In *T. mollissima* and *T. hatcheri* the cilia striking taper from base to apex, and are formed of much more elongated cells (to 15–19× as long as in basal diam.) and distal cilium cells are smooth or obscurely striolate.

Trichocolea mollissima (Hook.f. & Taylor) Gottsche

[Plate 4B, D; Figs. 26, 27]

Jungermannia mollissima Hook.f. & Taylor, London J. Bot. 3: 390. 1844. *Trichocolea mollissima* (Hook.f. & Taylor) Gottsche, Ann. Sci. Nat. Bot. V. l: 132. 1864. Type: Auckland Is., *Hooker*.
Trichocolea elegans Colenso, Trans. & Proc. New Zealand Inst. 20: 251. 1888 (1887), *non T. elegans* Lehm., Nov. Min. Cogn. Stirp. Pug. 10: 8. 1857. Type: New Zealand, Waipawa Co., Norse-

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lamina cells, abaxial view (S = sinus between lobes; note branched cilia originating from abaxial face of lamina; note also surface detail shown in part for lamina and cilia cells). 6. Cilium from lateral margin of leaf lobe, surface detail not shown (drawn at same scale as fig. 3). 7. Portion of stem paraphyllium. 8. Cilium of stem paraphyllium, papillae on surface not shown. (All from type.)

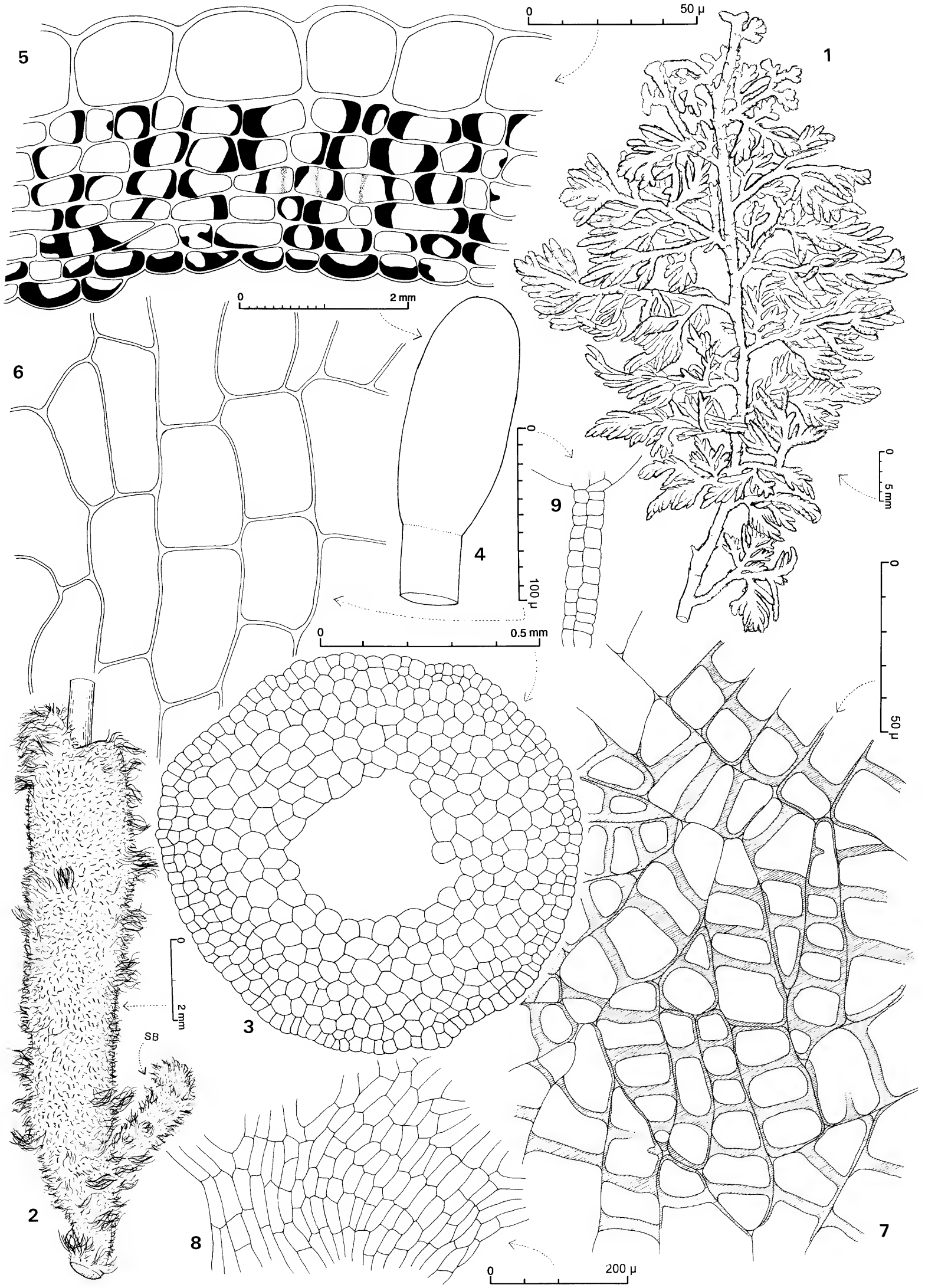

Fig. 26.
Trichocolea mollissima (Hook.f. & Taylor) Gottsche. 1. Habit; note 3-pinnate branches. 2. Coelocaule with portion of seta (SB = subfloral branch). 3. Seta, cross section; note hollow central area.

wood, 1886, ?*Colenso*; *ibid.*, Waipawa Co., near Dannevirke, May 1887, *Colenso*; *ibid.*, Hawke's Bay Co., Glenross, October 1887, *Balfour*.

Trichocolea australis Steph., Sp. Hepat. 4: 62. 1909. Type: New Zealand, *sin. coll.*

Plants with an aspect of a plumosely branched pleurocarpous moss, ascending or, when arboreal, pendulous, pale yellowish green to ± pale cream, robust, to 3.5 cm wide, including branches. Branches regularly 3-pinnate, tertiary branches uniformly arising from lowest secondary branches, the leading axis retaining its dominance, the main branches progressively less vigorous, the primary branches widely spreading; in suberect, particularly vigorous plants the pinnae drooping, convex and oriented perpendicular to plane of main axis. Branches julaceous, with a woolly appearance, with all sides appearing as a mass of interwoven cilia. Stems stiff, paraphyllia present, often dense, often branched, with cells similar to those of leaf cilia. Rhizoids usually absent. Leaves of stem firmly attached, stiffly and widely spreading but with lobes and cilia arching toward shoot apex, the leaf thus somewhat hand-like, the leaves *in situ* often appearing as a dense, brushed fringe of cilia, the individual lobes hardly discernible, the leaves on the stem distant to approximate, becoming imbricate on branches, semiamplexicaul, the insertion transverse to weakly succubous, suborbicular to subreniform, divided into 4–6 erect, pinnulate lobes (the lobes in ventral sector of leaf weakly larger), each lobe actually unequally (2)3-fid, consisting of a stronger, erect, regularly pinnulate division and 1–2 small, irregular, abaxially displaced, accessory divisions that are (1)2–4 cells wide at the base, and arched in same direction as main lobes, the divisions armed with pairs of opposing branched cilia. Lobes caudate, usually ± distinctly pinnulate (best seen in adaxial view), with numerous capillary segments and cilia, the ventral lobes 2–5 cells wide at base, with 2–3 tiers of laterally juxtaposed cells basal to the uniseriate row of 5–6(7) cells; cells of uniseriate row tapering, with swollen, dilated septa, thick-walled, becoming progressively longer and narrower toward lobe apices and ultimately becoming capillary, the surface finely striolate-papillose, the penultimate cell 10–12 μm wide × 60–98 μm long; terminal cell of uniseriate row often curved to sinuous, finely tapering to a sharp point, 7–12 μm wide, (90)100–150(170 or more) μm long, usually thick-walled in the tip, the surface smooth to finely striate-papillose; margins of lobes armed with pairs of opposing cilia, the cilia usually branched, often repeatedly, the armature in basal sector of lobe inserted on the abaxial surface of lobe and abaxially patent, the armature in distal sector of lobe ± in same plane as lobe, often appearing as if brushed in the same direction as the lobe; marginal cilia of lobe uniformly uniseriate throughout, the cells similar to those of the uniseriate sector of leaf lobes; sinus bases plane and not reflexed. Disc weakly asymmetric, consisting of a low, wide strip 2–5 cells high (from base to sinuses); margins of disc with branched cilia similar to those of lobes, the cilia sometimes abaxially displaced and lying at right angles to the disc plane. Cells of disc ± thick-walled, rarely with small trigones, the cells elongated, in somewhat regular tiers, in lamina middle 14–24 μm wide × 34–54 μm long; surface long-striolate, with only a few papillae. Oil-bodies pale

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4. Capsule profile. 5. Capsule wall, cross section. 6. Capsule wall, outer layer. 7. Capsule wall, inner layer. 8. Disc of ♂ bract, dorsal sector to right. 9. Antheridial stalk. (Fig. 1, from *Engel 17945*, New Zealand, South Is., Westland EP, between confluence of Jackson R. and Arawata R. and Lake Ellery; 2, from *Engel 18034*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, summit area of Haast Pass; 3–7, from *Engel 18489*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Bealey R.; 8, 9, from *Engel 18942*, New Zealand, South Is., Westland EP, near Waiho R. between Lake Wombat Terrace and Canavans Knob.)

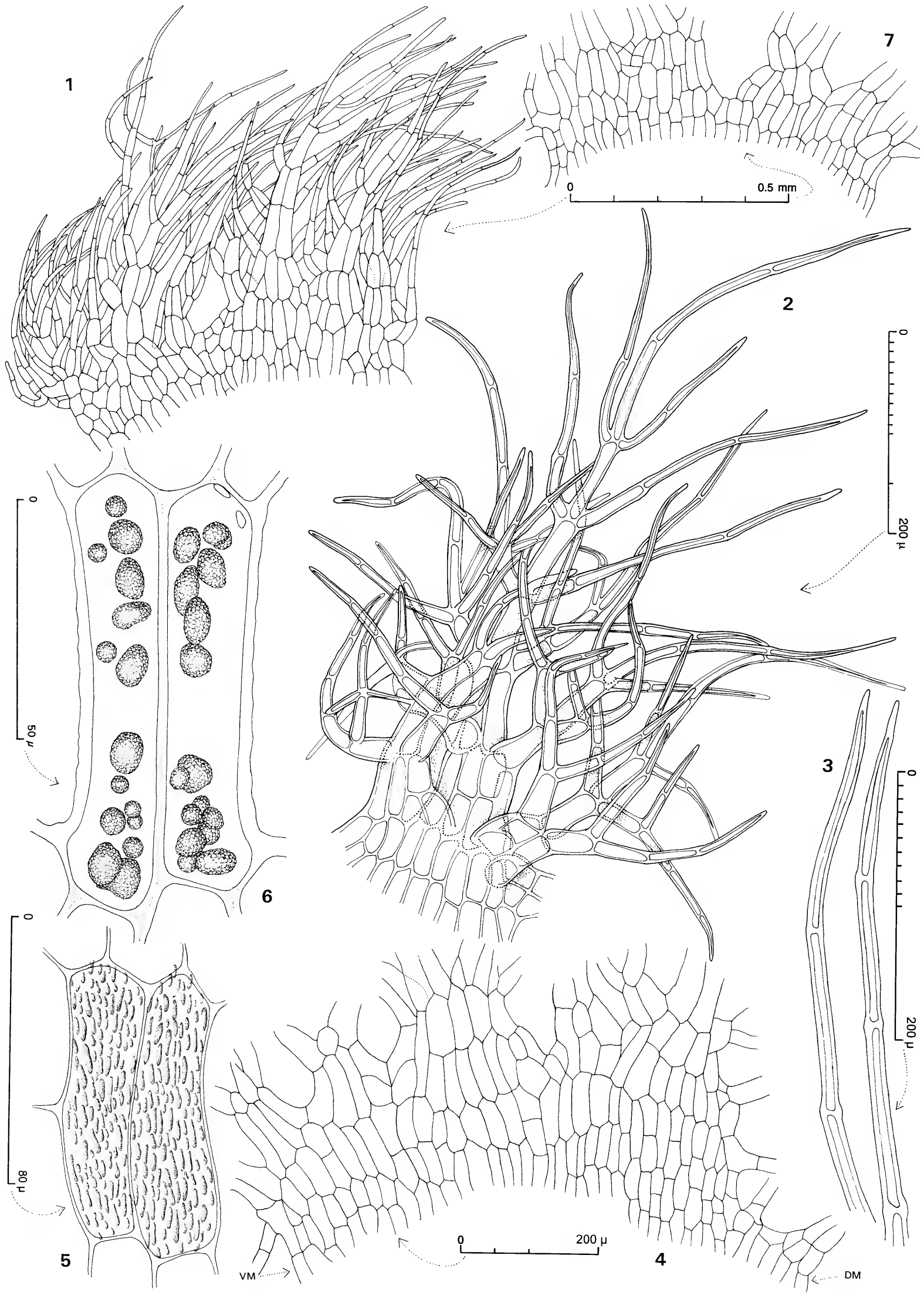

Fig. 27.
Trichocolea mollissima (Hook.f. & Taylor) Gottsche. 1. Leaf. 2. Leaf segment and 2 accessory divisions, abaxial view. 3. Distal sectors of 2 leaf lobes. 4. Leaf disc (VM = ventral margin; DM =

smokey grey, the paired cells at lobe bases with 11–15(20) per cell, irregularly granular-papillose, the tiny spherules distinct but faint and variable in size, the oil-bodies irregular in shape: subglobose to ovoid to broad-elliptic, some potato-shaped and with irregular bulges, 4.8–6.2 × 7.7–10.6 μm, spherical ones 3.8–6.7 μm in diam. Underleaves somewhat smaller than leaves, free or narrowly connate on one side, subreniform, quadrifid, the median sinus often deeper (then bisbifid), the armature similar to leaves; disc 3–4 cells high, at times 2 cells high below median sinus. Fungal partner absent.

Androecia intercalary on primary and secondary branches, hardly differentiated, the bracts divided to ca. 0.7–0.8, similar to leaves except somewhat ventricose at base and the disc higher dorsally, the abaxial face of lamina devoid of surface armature; antheridia large for bract size, 1–2 per bract, the stalk to ca. 18 cells long, biseriate. Coelocaule on main shoot or short to rather long branches, but becoming axillary or pseudolateral (through development, respectively, of 2 or 1 subfloral branches), the coelocaule cylindrical to narrowly clavate, densely paraphyllose.

Seta becoming hollow at maturity, ca. 21 cells in diam., the epidermal cells in numerous rows, smaller, the inner cells gradually becoming larger toward seta middle. Capsule ellipsoidal, the wall 78–92 μm thick, of 7–8 layers; outer layer of cells large, hyaline, ephemeral, lacking thickenings; innermost layer with very irregularly oriented, various-sized cells, with semiannular bands common, rather narrow, usually complete, rarely forked.

Spores 13.5–13.9 μm in diam., with low but sharply defined, close papillae and short-vermiculate markings. Elaters somewhat contorted, bluntly pointed at the ends, short, 8.6–11.9 μm wide, bispiral, the spirals 3.8–4.2 μm wide.

Distribution and Ecology: New Zealand: Auckland Islands, Campbell Island, Stewart Island (0–340 m), South Island (0–915 m), North Island (150–1040 m), Chatham Islands (160–260 m); Australia: Tasmania, Victoria, New South Wales. In New Zealand known from Rakiura (Stewart Island, Solander Island), Fiordland, Southern North Island, Volcanic Plateau, Taranaki, Gisborne, Auckland and Northland EPs.

Common throughout our area in a variety of forest types from sea level to ca. 950 m, especially those that are rich and particularly wet. It occurs on the forest floor often in damp leaf litter (then erect), in often thick masses on logs that are totally bryophyte covered, on old stumps and tree bases (then horizontal to ± pendulous), on tree-fern trunks, and on bryophyte-covered banks (at times along stream courses). It tolerates particularly wet, terricolous niches such as mucky soil in boggy areas, etc. It also may be arboreal (hosts include *Nothofagus menziesii*, *Weinmannia racemosa* and *Neomyrtus pedunculatus*) and is then pendulous in hanging sheets of bryophytes. It is occasional on vertical rock walls, rock ledges, or wet rock faces (especially where some soil and decaying vegetation have accumulated). Also in relatively open, boggy areas where it occurs at the sides of wet depressions and on bryophyte-covered banks. Accompanying species are *Adelanthus falcatus*, *Breutelia pendula*, *Canalohypopterygium tamariscinum*, *Cratoneuropsis relaxa*, *Cyathophorum bulbosum*, *Dicranoloma billardierei*, *Distichophyllum pulchellum*, *Heteroscyphus billardierei*, *Hypnodendron comosum*, *Leptotheca gaudichaudii*, *Lepidogyna hodgsoniae*, *Lepidozia pendulina*, *L. spinosissima*, *Lepidolaena*

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dorsal margin). 5. Cells of disc showing surface papillae. 6. Basal cells of leaf lobes with oil-bodies. 7. Underleaf disc. (Figs. 1–5, 7, from *Engel 18637*, New Zealand, South Is., Fiordland EP, track to Island Lake; 6, from *Glenny 8853*, New Zealand, South Is., Canterbury EP, Arthur's Pass, McGrath Creek.)

palpebrifolia, *L. taylorii*, *Metzgeria leptoneura*, *Plagiochila circinalis*, *P. gigantea*, *P. incurvicolla*, *P. lyallii*, *P. retrospectans*, *P. stephensoniana*, *P. strombifolia*, *Ptychomnion aciculare*, *Pyrrhobryum mnioides*, *Temnoma pulchellum*, *Thuidium furfurosum* and *Weymouthia cochlearifolia*.

Comments: Smaller, weakly developed plants may be confused with *Trichocolea hatcheri*, and must be identified with care. Also, hygrophilous plants growing on mucky soils often appear "etiolated" and spindly and have fewer tertiary branches. In such phases cells of the cilia have only slightly thickened walls, and have septa that are only slightly thickened. The cells of the uniseriate row, including the terminal cell, are often more papillose. The terminal cell tapers, but is narrowly rounded and neither sharp nor thickened at the tip. The terminal cell, however, is long and narrow, as in more well-developed material of the species.

Most often confused with *Lepidogyna hodgsoniae* as the two species are about the same size and can occur in similar niches in forest, are often the same yellow-green color, are both regularly 3-pinnate, and both ciliate. *Trichocolea mollissima* lacks lobules, and the cilia are branched while in *Lepidogyna* they are unbranched.

For the confusion in names applied to this species and *Trichocolea hatcheri*, see under that species.

Trichocolea hatcheri E.A.Hodgs.

[Plate 4C; Fig. 28]

Trichocolea hatcheri E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 69. 1965. Holotype: New Zealand, North Is., Roto-Kui Bush, east of Taupo, 1934, *Allison 7558* (MPN ex herb. Hodgson 7558, *non vidi*).

Trichocolea novaezelandiae R.M.Schust., J. Hattori Bot. Lab. 26: 265. 1963, *sin. descr. lat.*

Plants closely prostrate to adnate, compact and densely interwoven, deep green, velvety, small, 1–1.6 cm wide, including branches. Branches regularly 2-pinnate, tertiary branches rare, the leading axis retaining its dominance; branches julaceous, with a woolly appearance, with all sides appearing as a mass of interwoven cilia. Stems stiff, paraphyllia few or altogether lacking. Rhizoids usually absent, when present, long for plant size. Leaves of stem widely spreading but with lobes and cilia broadly arching toward shoot apex, the leaf thus somewhat hand-like, the leaves *in situ* often appearing as a dense fringe of cilia, the individual lobes often quite discernable, the leaves on the stem distant to approximate, becoming imbricate on branches, semiamplexicaul, the insertion transverse to weakly succubous, suborbicular to subreniform, 500–650 μm wide, 300–500 μm long, divided into 4–5 erect, pinnulate lobes (the lobes in ventral sector of leaf weakly larger), each lobe actually unequally (2)3-fid, consisting of a stronger, erect, pinnulate division and 1–2 small, irregularly branched, abaxially displaced, accessory divisions that are (1)2(3) cells wide at the base and feebly to distinctly arched in same direction as main lobes, the divisions armed with pairs of opposing branched cilia. Lobes caudate, somewhat irregularly pinnulate (best seen in adaxial view), with numerous segments and cilia, the ventral lobes 2–4 cells wide at base, with 2 tiers of laterally juxtaposed cells basal to the uniseriate row of 5–6 cells; cells of uniseriate row ± tapering, rather thin-walled, with only slightly thickened septa, somewhat longer and narrower toward lobe apices but not ultimately becoming capillary, the surface finely striolate to often distinctly papillose, the penultimate cell 10–12 μm wide × 41–60(72) μm long; terminal cell of uni-

seriate row ± straight, not curved to sinuous, slightly tapering to a ± rounded apex, 7–11 μm wide, but the length variable: 55–85(100) to 100–150 μm, usually thin-walled in the tip, the surface smooth to finely papillose; margins of lobes armed with pairs of opposing cilia, the cilia usually branched, often repeatedly, the armature all inserted on the abaxial surface of lobe and abaxially patent; marginal cilia of lobe uniformly uniseriate throughout, the cells similar to those of the uniseriate sector of leaf lobes; sinus bases plane and not reflexed. Disc weakly asymmetric, consisting of a low, wide strip 2–3 (very locally 4) cells high (from base to sinuses); margins of disc with branched cilia similar to those of lobes, the cilia sometimes abaxially displaced and lying at right angles to the disc plane. Cells of disc uniformly slightly to distinctly thickened, in somewhat regular tiers, in lamina middle 14–24 μm wide × (30)36–50(58) μm long; surface long-striolate, rarely with a few papillae. Underleaves somewhat smaller than leaves, free, subreniform, quadrifid, the armature similar to leaves; disc 2–3 cells high.

Androecia intercalary on primary branches and sometimes also the main shoot, the bracts divided to ca. 0.3–0.5, the lamina strongly ventricose, the abaxial face with ciliiform, unbranched processes (at times sparsely developed), the bract lobes similar to those of leaves; antheridia large for bract size, 1 per bract, the stalk biseriate. Coelocaule on main shoot or short to leading branches, but becoming axillary or pseudolateral (through development, respectively, of 2 or 1 subfloral branches), the coelocaule stoutly to longly and narrowly clavate, densely paraphyllose.

Capsule (only old valves with ± collapsed cells seen), the wall of (?)6 layers; epidermal layer of large, hyaline ephemeral cells lacking thickenings; innermost layer of cells with semiannular bands common, rather narrow, usually complete, rarely forked.

Spores 11.9–14.4 μm in diam., with low, rather well-defined, close papillae and short-vermiculate markings. Elaters bluntly pointed at the ends, 11–11.9 μm wide, somewhat contorted, bispiral, the spirals 1.9–2.4 μm wide.

Distribution and Ecology: New Zealand: Stewart Island, South Island (30–600 m), North Island (100–425 m), Chatham Islands (80–160 m); Australia: Queensland. In New Zealand known from Otago (Dunedin), Westland (near Westport, Mahinapua), Sounds–Nelson (Pelorus Sound), Southern North Island, Taranaki, Volcanic Plateau, Gisborne, Auckland and Northland EPs.

Occurring sporadically throughout its range, but most common in the eastern North Island. Found under a variety of lowland forest types that include *Beilschmiedia tawa*, *Weinmannia racemosa*, *Melicytus ramiflorus*, *Nothofagus fusca*, *N. menziesii*, *Prumnopitys taxifolia* and *Dacrycarpus dacrydioides* in sites ranging from very damp sites in stream courses to dry overhanging banks. Found on rotten logs, soil, tree roots, tree stumps, thin soil over rock, rarely epiphytic on *Dicksonia squarrosa* and (on Chatham Island) *Dracophyllum arboreum.* It may be corticolous, e.g., on trunk of *Weinmannia* at sea level to ca. 45 m in a narrow stream system with a canopy of *Weinmannia racemosa* at Port Pegasus, Stewart Island or, in the North Island, on the base of *Rhopalostylis sapida* (Kiwanis Reserve, N edge of Herekino Forest area, ca. 60–80 m) in a mixed broadleaf forest dominated by *Beilschmiedia* and *Vitex lucens*, with *Rhopalostylis*, *Coprosma*, *Dacrycarpus* and *Hoheria*. It occasionally occurs over shaded rock, e.g., on the summit of ridge at Bream Head (SE of Whangarei, 425 m) in a scrubby forest with a few large *Dysoxylum* and *Beilschmiedia*, but with much *Coprosma*, *Rhopalostylis*, *Hoheria* and climbing *Metrosideros*. The species ranges as far north as Radar Bush (WSW of Cape Reinga) at ca. 100 m in a forest of *Beilschmiedia – Vitex – Hoheria* and *Cyathea dealbata*.

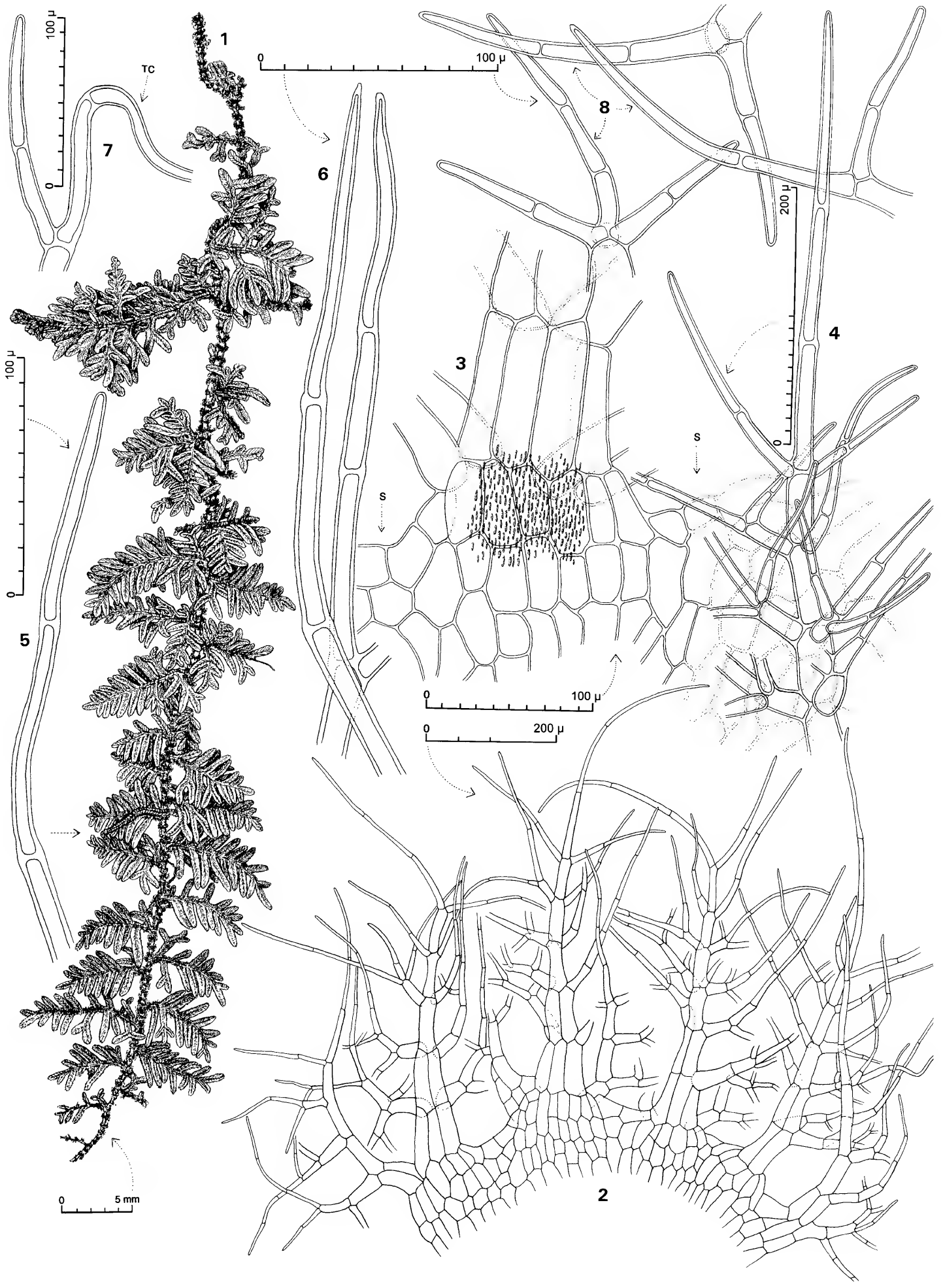

Fig. 28.
Trichocolea hatcheri E.A.Hodgs. 1. Plant, dorsal view (note epiphyllous hepatic [*Lejeuneaceae*], at arrow). 2. Leaf, adaxial view (some of cilia shown only in part for clarity). 3. Median lamina cells and 2 lobe bases, adaxial view, surface detail shown in part (S = sinus between lobes). 4. Distal portion of leaf lobe (abaxial view). 5, 6. Apices of leaf lobes. 7. Distal-most cilium of leaf lobe (TC = terminal cell of lobe). 8. Cilia from near base of leaf lobe. (All from *Schuster 67-1068*, New Zealand, North Is., Northland EP, SE of Kaitaia, Mangamuka Gorge Reserve.)

Species found with *Trichocolea hatcheri* are *Bazzania adnexa*, *Camptochaete angustata*, *Categonium nitens*, *Chiloscyphus muricatus*, *Cyathophorum bulbosum*, *Distichophyllum pulchellum*, *Fissidens asplenioides*, *Heteroscyphus coalitus*, *Hymenophyllum flabellatum*, *Leiomitra lanata*, *Lopidium concinnum*, *Pyrrhobryum bifarium*, *Racopilum convolutaceum*, *Radula buccinifera*, *R. grandis*, *Schistochila appendiculata*, *Telaranea herzogii*, *Temnoma pulchellum*, *Thuidium laeviusculum* and *Trichomanes venosum.*

Comments: Apart from its smaller size, appressed habit, and ± regularly bipinnate branching, there is little to distinguish *Trichocolea hatcheri* vegetatively from *T. mollissima*. However, many of these smaller, appressed, bipinnate plants bear abundant and well-developed coelocaules, a fact that argues for maintaining these plants as distinct. Several characters are commonly associated with this smaller habit. The cells of the uniseriate portion of the leaf lobes are less tapered, have thinner walls with only slightly thickened septa, and often have a distinctly papillose surface. The terminal and penultimate lobe cells are usually shorter and less finely tapered than those of *T. mollissima*, and the terminal cell is narrowly rounded and not thickened in the tip. When ♂ plants are present the two species may be readily separated, with *T. hatcheri* having less deeply lobed bracts that are armed on the abaxial surface of the lamina, and the presence of androecia only on primary branches.

More easily distinguished from *Trichocolea mollissima* in the field than from dried specimens by its vivid green color and velvety appearance due to the cilia being chlorophyllose (in contrast to the paler yellow color of *T. mollissima*), and by its invariably prostrate habit. The terminal branches lack the open cage of leaves seen in *T. mollissima* because the leaves tend to lie flatter to the stem. *Trichocolea hatcheri* is a smaller, more compact plant than *T. mollissima*, with a quite different distribution and ecology. It tends to grow on thin mineral soil over rocks (sometimes with *Treubia lacunosa*) and grows closely creeping over the substrate. Even vigorous plants rarely exceed 3–5 cm long and are, usually, rather closely 2(3)-pinnate, with tertiary branches usually sporadic or rare.

There has been a confusion in names applied to this species and *Trichocolea mollissima*. Hatcher (1958) used the name *T. mollissima* for this taxon (*T. hatcheri*), and used the later name *T. australis* Steph. for the true *T. mollissima*. Schuster (1963b) proposed *T. novae-zelandiae* as a substitute for "*T. mollissima*" of Hatcher, but without the required Latin description. Hodgson (1965) subsequently described the species as *T. hatcheri*.

Trichocolea hatcheri belongs to a complex that includes *T. pluma*. The two species are similar, for example, in having 2(3)-pinnate branching and a leaf disc 2–3 cells high. *Trichocolea pluma* differs from *T. hatcheri* in having a terminal cell of the leaf lobes that is rather thin-walled, ± parallel-sided throughout with a surface distinctly striate-papillose. In these respects *T. pluma* is more like *T. rigida*, and, moreover, like that species the tip cell of the leaf lobes is rounded at the summit. *Trichocolea pluma* may be distinguished from *T. rigida* by the regularly 2(3)-pinnate branching, by the straight or dilated septa of the cells in the cilia and by the lower leaf disc.

Eotrichocolea R.M.Schust.

Eotrichocolea R.M.Schust., J. Hattori Bot. Lab. 26: 252. 1963.

Plants ± prickly in appearance, anisophyllous, rather rigid, rather closely procumbent to ascending, light yellow-green, small, usually to only 2 cm long. Branching typically 1-pinnate

(sporadically 2-pinnate), the branches irregularly arranged, nearly all of *Frullania* type, of limited length, cernuous, tapered, ultimately becoming flagelliform and microphyllous; *Acromastigum*-type branches rare. Stem rather large for plant size and notably more robust than the branch axes, paraphyllose, the paraphyllia 2–3(4)-celled, the cortical cells thin-walled, the medullary cells of similar size, also thin-walled. Leaves obliquely spreading, distant to contiguous, ± transverse to weakly to distinctly incubous, ± symmetrical, ca. 600–700 μm wide × 600–800 μm long, deeply quadrifid (lateral lobes slightly to markedly smaller), the lobes 2–4 cells wide at base, terminating in tapered cilia each comprised of a uniseriate row of 3–5 cells; margins of lobes with (1)2–5 cilia arranged alternately or (often) opposed, the armature often displaced and inserted on the abaxial surface of lobe and stiffly abaxially patent, the lateral cilia rather rigid, spiniform, tapered as in lobes, consisting of a uniseriate row of 2–3(4) cells; disc 2–3(4) cells high, the margins with short cilia. Cells moderately elongated (to 2:1 in disc, to 6:1 in lobes), with walls thin to somewhat firm, the surface of lobes conspicuously papillose, of disc distinctly and closely striolate-papillose. Oil-bodies pale smokey grey, the paired cells at base of uniseriate row of the lobes with 5–9 per cell, the uniseriate row with 8–12 per cell, the basal row of disc with 4–5 per cell, 6–7(9) per cell of next row up in the disc, the oil-bodies coarsely granular-papillose, the granules well defined, not protruding beyond the membrane, the oil-bodies subglobose, almost spherical but slightly distorted, ovoid, the larger ones less spherical and 7 × 10 μm, the spherical ones 6–7 μm in diam. Underleaves ca. 0.5× leaf size, deeply bifid, the lobes 2–3(4) cells wide at base, terminating in a uniseriate row of 3–4 cells, the lobes with a few, often opposed, marginal cilia similar to those of leaves and like them often abaxially displaced, the cilia at times with a marginal sessile slime papilla; disc 1–2 cells high. Asexual reproduction absent.

Dioecious. Androecia on main shoot, becoming intercalary; bracts not much differentiated from leaves, the disc somewhat concave; antheridia 1 per bract, the stalk short, biseriate. Gynoecia terminal on leading shoots; bracts leaf-like, inserted near coelocaule base as well as just beyond the coelocaule midpoint. Coelocaule clavate, the wall polystratose, bearing the bracts and variable paraphyllia, but with much of coelocaule surface exposed; perianth lacking, at times several larger, ciliate leaves are present near coelocaule apex, which may represent perianth vestiges; free calyptra absent, the unfertilized archegonia at coelocaule summit.

Foot massive, conoidal. Seta long, rather massive, becoming hollow at maturity. Capsule short-ellipsoidal, dehiscence irregular, the valves irregular in size and shape and tending to fragment with age, the wall 4–5-stratose; outer layer of cells large, hyaline, without pigmented thickenings; innermost layer of cells with complete or incomplete semiannular bands.

Spores and elaters unknown.

Type: *Eotrichocolea polyacantha* (Hook.f. & Taylor) R.M. Schust. (≡ *Jungermannia polyacantha* Hook.f. & Taylor)

Eotrichocolea is monotypic. It differs from *Trichocolea* in general aspect, as well as several other features that include the incubous leaves, the irregular capsule dehiscence, the 4–5-layered (vs. [5]6–8-layered) capsule wall, and the sporadic ability to develop *Acromastigum*-type branches. The presence of drooping, tapered and ultimately flagelliform terminal branches is also distinctive vs. branches that spread ± in the same plane as the main shoot and that do not taper or become flagelliform toward the tips. Also, the ecology of *Eotrichocolea* is quite different, often occurring sparingly as isolated plants.

References: Schuster (2000a, 2001d).

Eotrichocolea polyacantha (Hook.f. & Taylor) R.M.Schust.

[Plate 4A; Fig. 24: 4, oil-bodies, p. 178]

Jungermannia polyacantha Hook.f. & Taylor, London J. Bot. 3: 390. 1844. *Trichocolea polyacantha* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 238. 1845. *Eotrichocolea polyacantha* (Hook.f. & Taylor) R.M.Schust., J. Hattori Bot. Lab. 26: 252. 1963. Type: Auckland Is., *Hooker*.

Distribution and Ecology: New Zealand: Auckland Islands, Campbell Island (60 m), Stewart Island (330–530 m), South Island (530–1370 m), North Island (1240 m); Australia: Tasmania. In New Zealand known from Southland (Eyre Mtns.), Westland, Western Nelson (Stockton) and Volcanic Plateau EPs.

On Stewart Island the species apparently does not occur below 330 m. On Mt. Rakeahua (track to summit, 500 m) plants occurred in a moderate terrace with mosaic communities consisting of penalpine cushion vegetation, prostrate *Leptospermum scoparium* and *Olearia colensoi* to 1 m tall. At this site the species grew scattered and in small tufts in a mound of bryophytes consisting of *Acromastigum* and *Bazzania* under a canopy of 1 m tall *L. scoparium*. Also at the summit of Pryse Peak (330–340 m), in open forest in a plateau area with vegetation that includes stunted *Dacrydium cupressinum*, *Podocarpus hallii*, *Olearia colensoi*, *Gahnia*, *Blechnum* and bryophyte cushions on the forest floor. Here the species grew on a raised mound, atypically forming a ± pure colony and loose cushion under a canopy of *Gahnia*.

In Fiordland the species occurs in the transition from *Nothofagus menziesii* forest to the alpine. In Westland growing through litter and other bryophytes, in fault ditches, sinkholes, and constantly damp south-facing hillslopes in penalpine tussockland (of *Chionochloa pallens* or *C. australis*) and *Olearia colensoi* shrublands; with *Bazzania adnexa*, *Blepharidophyllum vertebrale*, *Cryptochila pseudocclusa*, *Dicranoloma obesifolium*, *Distichophyllum pulchellum*, *Gackstroemia alpina*, *Heteroscyphus mononuculus*, *Hymenophyllum multifidum*, *Lepidozia ornata*, *Marsupidium surculosum*, *Megaceros giganteus*, *Metahygrobiella drucei* and *Schistochila monticola*. Near the summit of Haast Pass (530 m) occurring scattered through other bryophytes (including *Temnoma*, *Triandrophyllum*, *Chiloscyphus*, *Lepidozia*) on a wet cliff under *Nothofagus* forest at the roadside. In the North Island under low *Nothofagus solandri* var. *cliffortioides* forest with steep, moist, peaty, mossy banks in valley of small side stream below small waterfall at ca. 1200 m (Mangawhero River, off Ohakune Mtn. Road, Tongariro Natl. Park).

The species has a scattered distribution, but because plants for the most part occur sparing and isolated, and hence easily overlooked, it probably will eventually be found to be less rare.

Comments: *Eotrichocolea* has a distinctive aspect. Plants are small and prickly in appearance and typically 1-pinnate. The frequent occurrence as isolated or sparingly tufted plants is notable, and shoots vary from closely procumbent and with the flagelliform branch tips geotropic and "rooting" in the substrate to suberect. The combination of large and fleshy main shoot and much narrower terminal branches that are cernuous and flagelliform distally is also distinctive. Antheridial stalks are biseriate and not uniseriate as stated in Schuster (2000a).

The species most closely resembles *Trichotemnoma corrugatum*, but with narrower shoots, stems with paraphyllia, leaves remote and weakly incubous (not succubous as in *T. corrugatum*).

Suborder 4. **LEPIDOZIINEAE** R.M.Schust.

Jungermanniales subord. *Lepidoziineae* R.M.Schust., J. Hattori Bot. Lab. 26: 228. 1963.

Three families are included in the *Lepidoziineae*: *Phycolepidoziaceae*, which is monotypic and contains only the Neotropical genus *Phycolepidozia* R.M.Schust.; *Lepidoziaceae*, which is well represented in our area; and *Calypogeiaceae*, which is represented in New Zealand by two species in the genera *Calypogeia* and *Mnioloma*.

Family **LEPIDOZIACEAE** Limpr.

Lepidoziaceae Limpr. *in* Cohn, Krypt.-Fl. Schlesien 1: 310. 1875 ("Lepidozieae").
Zoopsidaceae Nakai *in* Ogura, Ord. Fam. Trib. Gen. Sect. ... nov. ed. 199. 1943.
Bazzaniaceae Nakai *in* Ogura, Ord. Fam. Trib. Gen. Sect. ... nov. ed. 200. 1943.
Hyalolepidoziaceae Fulford, Mem. New York Bot. Gard. 11: 376. 1968.
Regredicaulaceae Fulford, Mem. New York Bot. Gard. 11: 358. 1968.
Paracromastigaceae Fulford, Mem. New York Bot. Gard. 11: 384. 1968.

Plants with gametophytes highly variable, normally leafy and isophyllous to strongly anisophyllous, thallose in a few genera, the plants erect to creeping, typically green, sometimes developing brown or fuscous pigments (never with reddish pigmentation), robust to minute. Branching plastic, variable, often abundant and regular, at times 1–2(3)-pinnate or-pseudo-dichotomous, the branches often of *Frullania* type, occasionally also of *Microlepidozia* or *Acromastigum* types; intercalary branches also present, often ventral, sporadically lateral; nearly always with geotropic stoloniform or flagelliform branches. Stems with cortex variably differentiated, the diameter of cortical cells normally slightly to greatly larger than those of medullary cells, a hyalodermis formed in some taxa. Rhizoids from stem in fascicles at underleaf bases, occasionally from underleaf disc cells, also at bases of leaves of microphyllous branches. Leaves normally large and well developed, vestigial and 1- or few-celled in a few genera, the insertion variable: transverse to incubous to succubous, the lines of insertion extending to stem midline dorsally or not reaching the stem midline and delimiting a leaf-free strip of stem cells; leaves 3–4-fid ranging to, less often, 5–12-fid by typically entire lobes, at times bifid, exceptionally unlobed, the leaf margins mostly entire, rarely ciliate. Cells variable, thin- to thick-walled, trigones small to large, rarely large and knot-like or altogether lacking; surface variable: smooth or finely to coarsely papillose, or glaucous, waxy and water-repellent. Oil-bodies present, granular to botryoidal, absent in various taxa. Underleaves often 3–4 or more lobed, sometimes unlobed, in some taxa present as 1- or 2-celled vestiges, but a distinct ventral merophyte at least 2 cells wide present in all taxa. Asexual reproduction, if present, by tubers in various taxa, by fragmenting lobe tips (e.g., *Telaranea*, *Kurzia*, *Lepidozia*) or by caducous leaves (*Bazzania*), never by gemmae.

Dioecious in most taxa, sporadically autoecious. Androecia typically on short, spicate ventral-intercalary branches from leading shoots, exceptionally terminal on short to moderately long *Frullania*-type branches; bracts often moderately to markedly smaller than sterile leaves, usually monandrous, the antheridial stalk 1- or 2-seriate; bracteolar antheridia rare. Gynoecia nearly exclusively on abbreviated ventral-intercalary branches lacking normal vegetative leaves, rarely on lateral-intercalary branches or terminal on leading shoots. Bracts and bracteoles similar (the gynoecia triradial), in 2–several series, usually larger and different from leaves and underleaves, dentate to lobulate to (often) shallowly to deeply lobed. Perianth fusiform, often terete below and bluntly trigonous above, tapered to the mouth, comprised of ± elongated cells; mouth variable, denticulate to shallowly lobulate to more often laciniate or ciliate.

Seta with (4), 8, 12, or 16 rows of epidermal layers, the inner cells smaller, 16–24(34) to 12 or fewer, rarely as few as 6 or 4. Capsule ellipsoidal to obloid, the valves erect, nonspiral, the wall 2–5(6)-layered; outer layer of cells ± tiered, rectangular, with two-phase development, the primary longitudinal and all transverse walls normally lacking pigmented thickenings, alternating with the secondary (longitudinal) walls with conspicuous radial (nodular) thickenings; inner layer of cells with weak to distinct semiannular bands.

Spores papillose-vermiculate or reticulate-areolate, 1–3× elater diam. Elaters bispiral, blunt-tipped.

Type: *Lepidozia* (Dumort.) Dumort.

Schuster (2000a) recognized eight subfamilies. One of these, the *Neogrolleoideae*, was removed by Engel and Braggins (2001) and placed in an independent family, *Neogrolleaceae*. One subfamily, the *Megalembidioideae*, was added (Engel and Braggins, 2005). The eight subfamilies are as follows, the first six occur in New Zealand:

1) Subfam. *Lepidozioideae*, with six genera, five of which occur in New Zealand. The sixth, *Sprucella* Steph., has two species, both in tropical–subtropical Africa.
2) Subfam. *Bazzanioideae* Rodway has four genera, two (*Bazzania*, *Acromastigum*) are larger genera that are widely distributed in the southern temperate zone, including New Zealand. One, *Dendrobazzania* R.M.Schust. & W.B.Schofield, is monotypic and is known only from Bhutan and the Queen Charlotte Islands. The other, *Mastigopelma* Mitt., has three species and occurs in Samoa, Borneo-Sarawak and the Louisade Archipelago.
3) Subfam. *Drucelloideae* (Boesen) R.M.Schust. has only the monotypic *Drucella* E.A. Hodgs., which occurs in our area.
4) Subfam. *Lembidioideae* R.M.Schust. has four genera, all with representatives in New Zealand.
5) Subfam. *Megalembidioideae* Engel has only the monotypic *Megalembidium* R.M.Schust. of New Zealand.
6) Subfam. *Zoopsidoideae* R.M.Schust. consists of eight genera, five of which occur in New Zealand. Of the extraterritorial genera, *Monodactylopsis* (R.M.Schust.) R.M.Schust. has two species, both of Brazil; *Odontoseries* Fulford is monotypic and is known only from Venezuela; and *Pteropsiella* Spruce has two Neotropical species from the Amazonian–Orinoco drainage.
7) Subfam. *Micropterygioideae* Grolle consists of two Neotropical genera, *Micropterygium* Lindenb., Nees & Gottsche, with ca. 18–19 species, and the monotypic *Mytilopsis* Spruce.
8) Subfam. *Protocephalozioideae* R.M.Schust. has only the monotypic *Protocephalozia* (Spruce) Goebel of the Neotropics.

Subfam. ***Lepidozioideae***

Lepidozia (Dumort.) Dumort.

Pleuroschisma sect. *Lepidozia* Dumort., Syll. Jungerm. Europ. 69. 1831.
Lepidozia (Dumort.) Dumort., Recueil Observ. Jungerm. 19. 1835, *nom. cons.*
Herpetium sect. *Lepidozia* Nees, Naturgesch. Eur. Leberm. 3: 31. 1838.
Lepidoziopsis E.A.Hodgs., Rec. Domin. Mus. 4: 105. 1962.

Plants anisophyllous, firm, creeping to loosely prostrate to, more often, somewhat ascending, rarely stiffly erect, yellowish or whitish to olive-green, rarely brownish in life, rarely glaucous, medium-sized to vigorous, usually 0.5–2.5(4) mm wide. Branching irregular to regular, copiously 1- to 2- or 2–3-pinnate, of *Frullania* type, the lower terminal branches partly or mostly attenuate at the apices, often becoming rhizoid-bearing; *Acromastigum*-type branching present in a few species; *Microlepidozia*-type branches lacking; ventral-intercalary microphyllous or leafy branches in some taxa; lateral-intercalary branches lacking. Stem firm to rigid, with (18)20–32 or more rows of firm-walled cortical cells, typically little or at most moderately larger in diameter than those of adjoining medulla, not forming a discrete hyaloderm; subepidermal layers occasionally present, composed of thick-walled cells; medullary cells equal to or slightly smaller than cortical, firm-walled (the outer sometimes strongly so). Rhizoids of normal-leaved axes usually rare or absent, except at shoot bases, arising from underleaf bases; rhizoids on flagelliform shoots from all three merophyte rows. Leaves almost without exception 4-lobed or 4-lobulate on main shoots, incubous to subtransverse, the insertion extending to stem midline dorsally, the leaves typically asymmetrical, the dorsal half (and dorsal 1–2 lobes) larger than the ventral, the lobes usually many-celled (at bases 3–4 or more cells broad in most taxa), the cells similar to those of disc, the lobes usually sharp, often deflexed or inflexed in most taxa; disc margins entire or toothed to spinose-dentate or ciliate. Cells of disc irregularly arranged, not tiered, firm-walled, the lumina often rounded, the trigones concave-sided and mostly obscurely defined; median cells of disc mostly 18–25(40) μm wide; surface smooth or clearly papillose. Oil-bodies present in all leaf cells, colorless, usually (2)5–16 per cell, relatively large, usually botryoidal, less often subhomogeneous, often vestigial in subg. *Glaucolepidozia*. Asexual reproduction lacking or (*Lepidozia fugax*, occasionally in *L. digitata*) via fragmenting or caducous leaf lobes. Underleaves usually 0.5 or less the lateral leaves in area, transversely inserted, symmetrically 4-lobed on main shoots.

Dioecious, rarely (generitype, *Lepidozia reptans*) autoecious. Gametangial branches all short, devoid of normal leaves and underleaves, ventral-intercalary in origin (the androecia less frequently terminal on primary and secondary branches). Androecia typically spicate, smaller than vegetative shoots, the bracts concave, ± imbricate, lobed like (but usually more shallowly than) vegetative leaves; antheridia 1–2 per bract, the stalk 2-seriate; bracteoles small, lacking antheridia. Gynoecia with bracts and bracteoles identical, 4(6)-lobed to -lobulate, occasionally 2–4-dentate to -lobulate. Perianth fusiform or ellipsoidal-fusiform, bluntly trigonous in at least the narrowed distal sectors, the mouth usually crenulate to crenate-denticulate.

Seta with (8)12–16 large epidermal + 16 or more rows of much smaller internal cells. Capsule ellipsoidal to obloid, the wall 3–5(6)-layered; outer layer of cells often imperfectly tiered, the primary longitudinal and all transverse walls normally lacking pigmented thickenings, the secondary (longitudinal) walls with conspicuous radial (nodular) thickenings, often ± coalescing; inner layer of cells narrower, with radial (nodular) thickenings, ± connected by weak, often vestigial, tangential bands.

Spores papillose-vermiculate, less than 1.5× the diam. of the bispiral elaters.

Type: *Lepidozia reptans* (L.) Dumort. (≡ *Jungermannia reptans* L.), a Holarctic, widespread species.

Lepidozia is a large and polytypic genus, with perhaps ca. 80 species worldwide. Over half of these occur in an area extending from New Zealand (with 23 species) into Southeast Asia (e.g., New Guinea has ca. 17 species). Much of the morphological diversity found within the genus occurs in New Zealand. Of the seven subgenera of *Lepidozia*, five are present in New

Zealand (see Engel and Schuster, 2001; Schuster, 1973). Absent from New Zealand are subg. *Chaetolepidozia* R.M.Schust., which ranges from Costa Rica south to Colombia and Ecuador, and subg. *Cladolepidozia* R.M.Schust. of the Paleotropics.

The species show a diverse ecology: they occur principally on soil, peat, or decaying logs, but also on soil-covered rocks, rarely a few invade even the lower trunks of trees. The large bulk of taxa occur in sheltered loci, but several ascend into the alpine zone, where they occur in damp sites of alpine grasslands, or on soil in crevices of crags or cliffs. All of our species are unisexual, but ♂ and ♀ plants often occur intermingled, and in many species sporophytes are produced, if infrequently so.

References: Hodgson (1956); Engel and Schuster (2001); Engel (2004a).

Artificial Key to Species[1]

1a. Branching irregularly to regularly 1-pinnate (except *L. serrulata*), secondary branches rarely or sporadically developed, if present only 1(2) per primary branch (branches sometimes developing into new leafy shoots); leaves imbricate to contiguous, the insertion weakly to distinctly incubous 2

2a. Plants opaque and ivory-white, becoming pale brownish with age; leaves and stems with a dull, waxy, water-repellent surface (at least on new growth) 3

3a. Dorsal margin of leaf moderately to distinctly ampliate; cells of disc and lobes not papillose (but with a fine, granular coating); leaves broadly inserted and clasping the stem, distinctly concave, with involute lobes and margins; leaf insertion strongly incubous to horizontal 4

4a. Disc cells with evenly thickened walls, trigones never present; dorsal margin of leaf strongly ampliate, distinctly auriculate at the insertion, the dorsal margin sinuate to distantly toothed; leaf lobes subcaudate, ending in a uniseriate row of 3–5 cells. Rare (South Is.: Fiordland, Paparoa Ra.) . . . . . *L. glaucophylla* (p. 259)

4b. Disc cells lax, nearly thin-walled, trigones lacking to medium; dorsal margin of leaf moderately ampliate, ± clearly cordate at the insertion, the dorsal margin normally entire; leaf lobes acute to apiculate, ending in a single cell or a uniseriate row of 2–3(4) cells 5

5a. Plants medium, to 1.5 cm wide (including branches); leaves 0.8–1.3 mm long and broad, the disc 15–22 cells high at dorsal sinus, the median lobes 6–10 cells wide at base; underleaves inserted on 9–10 rows of stem cells, the disc 5–9 cells high; first branch underleaf 2- to 4-lobed, transversely inserted on the stem, often somewhat below the branch. Typically in upper montane forests to penalpine to alpine . . . . . *L. bisbifida* (p. 262)

5b. Plants small, to 0.6 cm wide (including branches); leaves at most 0.55 mm long and broad, the disc 7–13 cells high at dorsal sinus, the median lobes 3–5 cells wide at base; underleaves inserted on 3–4 rows of stem cells, the disc 2–4 cells high; first branch underleaf 2-lobed (or rarely undivided), obliquely inserted at branch base. Forest plant; 950–1390 m . . . . . *L. digitata* (p. 264)

[1]Modified from Engel and Schuster (2001).

3b. Dorsal margin of leaf ± straight; cells of disc and lobes striate-papillose, the papillae obscured by the continuous waxy coating; leaves narrowly inserted, the disc flat, with spreading lobes; leaf insertion weakly to distinctly incubous. Disc and lobe cells distinctly thick-walled; first branch underleaf undivided or 2-lobed (rarely 4-lobed). Chatham Is. + South Is. (150–300 m) + North Is. (Waipoua area, 340–540 m) . . . . . *L. glaucescens* (p. 266)

2b. Plants green, yellow-green, brownish to dark brown, but without a dull, waxy, water-repellent surface 6

6a. Dorsal margin of leaves serrate or dentate-laciniate or ciliate 7

7a. Dorsal pair of lobes caudate, the distal portion ciliiform and with a uniseriate row of 4–15 cells 8

8a. Branching 1-pinnate; dorsal margin of leaves with numerous (up to 19) spinose teeth or cilia; lobe margins often with paired cilia; underleaf lobes truncate, the summit with several cilia ± equal in size . . . . . *L. ulothrix* (p. 256)

8b. Branching 2-pinnate; dorsal margin of leaves denticulate-dentate; lobe margins entire or sparingly denticulate; underleaf lobes acute or if ± truncate, then with accessory cilia smaller . . . . . *L. serrulata* (p. 253)

7b. Dorsal pair of lobes acute to acuminate, the distal portion not ciliiform, the uniseriate row comprised of 2–3 cells 9

9a. Dorsal margin of disc and contiguous margin of lobe irregularly dentate to coarsely serrate; leaf lobes acute; underleaves divided to at most 0.5 (the disc 12–16 cells high), the lobe margins entire or sparingly toothed . . . . . *L. kirkii* (p. 248)

9b. Dorsal margin of disc and confluent margin of lobe ± regularly spinose-dentate, with discrete, often curved, acuminate spines; leaf lobes acuminate; underleaves divided to 0.55–0.8 (the disc 6–9 cells high), the lobe margins laciniate-multifid (rarely entire) . . . . *L. hirta* (p. 250)

6b. Dorsal margin of leaves entire (rarely with a basal tooth) 10

10a. Leaf lobes setaceous, terminating in a uniseriate row of 6–10(12) elongated capillary cells. Leaf insertion distinctly incubous; trigones large and bulging to knot-like; underleaves distinctly connate on one side . . . . . *L. setigera* (p. 209)

10b. Leaf lobes never setaceous, the lobes acute or terminating in a short uniseriate row of up to 2–5 cells 11

11a. Leaves appressed to stem, distinctly ventrally secund, ± equally and shallowly (0.25–0.4) lobed, the two median lobes wider than the outer lobes. Slender, wiry plants with strongly ventrally secund branches . . . . . *L. procera* (p. 211)

11b. Leaves spreading, not appressed to stem, the two median lobes not clearly wider than outer lobes. Leaves often asymmetrically lobed, the dorsal lobes often ± united in a perceptible pair, the ventral lobes usually shorter and often somewhat divergent from the dorsal pair 12

12a. Leaves and underleaves variously appendaged, with accessory lobes and often lamellae; underleaves plicate, the lobes ventrally sulcate, the sinus bases strongly reflexed. Plants brown; branches spreading. Penalpine–alpine species . . . . . *L. ornata* (p. 219)

12b. Leaves and underleaves not appendaged (rarely with marginal teeth); underleaves plane 13

13a. Plants with brown pigments, typically erect, with distinctly ventrally secund branches (occasionally greenish with spreading branches in var. *parvula*). Disc cells often distinctly thick-walled, brownish; leaf and underleaf lobes often bluntly rounded. Montane to alpine species . . . . . *L. obtusiloba* (p. 213)

13b. Plants green, typically prostrate to procumbent, with spreading or ± decurved branches 14

14a. Median cells of leaf disc large (26–41 mm wide); plants medium-sized; underleaves inserted on 10 rows of stem cells; leaves 0.8–1 mm wide × 0.6–0.9 mm long. Leaves variable in shape, the ventral lobes typically not much shorter than the dorsal (the branch leaves ± equally 4-lobed). Surface of leaf disc smooth; median disc-cells typically with trigones straight to large and bulging . . . . . *L. concinna* (p. 223)

14b. Median cells of leaf disc smaller: 25 μm wide or less (except sometimes in *L. bidens*); plants small to minute; underleaves inserted on 9 or fewer rows of stem cells; leaves usually less than 0.5(0.6) mm in longest dimension 15

15a. First branch underleaf consistently unlobed. South Is. (Westland Prov., 990 m) + North Is. (Rotorua area) 16

16a. Leaves deeply (0.5–0.6) quadrifid, the lobes lanceolate; dorsal sinus descending at least 0.5 leaf length; lobes ending in ± elongated cells, the lobe cells mostly rectangulate; first branch underleaf subulate; stem half-leaf usually 0.45–0.55 bifid; branch leaves mostly 3-lobed . . . . . *L. acantha* (p. 239)

16b. Leaves under 0.5 quadrifid, the lobes triangular, under 3× as long as broad; dorsal sinus usually descending to 0.2–0.3; lobes ending in non-elongated cells, the lobe cells mostly subquadrate; first branch underleaf ovate-lanceolate; stem half-leaf under 0.25 bifid; branch leaves 4-lobed . . . . . *L. elobata* (p. 241)

15b. First branch underleaf of mature shoots 2–4-lobed or mixed 1–2-lobed. Leaves mostly bis-bifid: median sinus deeper, dorsal sinus usually shallow, usually strongly asymmetric, the lobes always strongly unequal 17

17a. Leaves ± conspicuously papillose (at least on the lobes) or if indistinctly papillose (suboptimal populations of *L. laevifolia*) then the dorsal margin of disc ampliate and the outer wall of the marginal cells of disc and lobes not thickened 18

18a. Marginal cells of disc and lobes with free wall not differentially thickened; dorsal margin of disc ampliate, the margin cordate to auriculate at the insertion; leaves usually distinctly concave, wet or dry. Leaves coarsely papillose, the disc closely and distinctly striate-papillose; lobes with uniseriate row (when present) of non-elongated cells. Common; usually not below 300 m . . . . . *L. laevifolia* (p. 227)

18b. Marginal cells of disc and lobes with a strongly thickened free wall (the wall often bulging into the cell lumen); dorsal margin of disc ± straight to moderately ampliate proximally, cordate at insertion, not clearly auriculate; leaves plane or only moderately concave, the lobes spreading or incurved. Rare or infrequent species 19

19a. Lobe tips caducous, the cells turgid, barrel-shaped, the septa constricted; lobes with uniseriate row of 2–4(5) cells, the cells ± isodiametric, the terminal cell rounded at the tip; median disc cells 17–24 mm wide; underleaves inserted on 7 rows of stem cells. Margins of disc and lobes occasionally toothed. South Is., 560–900 m. . . . . *L. fugax* (p. 232)

19b. Lobe tips not caducous, the cells with straight or concave walls, the septa dilated; lobes terminating in a single cell or at most 2 superposed cells, the cells elongated (to 2:1), the terminal cell ± tapering to a point; median disc cells 11–16 μm wide; underleaves inserted on 4–6 rows of stem cells. South Is. + North Is.; forest species . . . . . *L. novae-zelandiae* (p. 237)

17b. Leaves smooth (rarely finely and indistinctly papillose); outer wall of marginal cells of disc and lobes distinctly thickened 20

20a. Plants medium-sized (the main shoots, 700–900 mm wide, leaf tip to leaf tip); underleaves inserted on 8 rows of stem cells; leaf disc 8–10 cells high at dorsal sinus, the cells ± longitudinally elongated; leaves with dorsal lobes ending in a uniseriate row of elongated (up to 2:1) cells. Plants of forests (0–330 m in South Is.; to 920 m in North Is.). . . . . *L. bidens* (p. 245)

20b. Plants minute to small (the shoots 365–490 μm wide, leaf tip to leaf tip); underleaves inserted on 5–6 rows of stem cells; leaf disc 9–12 cells high at dorsal sinus, the cells quadrate or slightly longer than wide; dorsal lobes with cells of uniseriate row ± isodiametric or at most slightly longer than wide. Plants of forests + penalpine zone + (var. *alpina*) alpine zone (570–1945 m); South Is. + North Is. . . . . *L. pumila* (p. 242)

1b. Branching regularly and consistently 2-pinnate, the branches slender and drooping; leaves typically distant, vertically oriented, the insertion transverse. Plants erect, with rigid, woody stems 21

21a. Leaves inconspicuous, scale-like, narrower than stem, strongly erect and commonly ± appressed to stem, divided to 0.4–0.5 (median sinus) . . . . *L. microphylla* (p. 204)

21b. Leaves conspicuous, wider than stem, stiffly patent or erect-patent from a spreading base, divided to 0.65–0.9 22

22a. Leaves ± symmetrical, the lobes 6–8 cells wide at base, ending in a uniseriate row of 7–12 cells; dorsal margin of disc straight to slightly concave; underleaf disc 3–6 cells high, the lobes with a uniseriate row of 7–16 cells . . . . . *L. spinosissima* (p. 201)

22b. Leaves asymmetrical, the lobes 14–24 cells wide at base, with a uniseriate row of 2–4(6) cells; dorsal margin of disc broadly ampliate; underleaf disc 14–24 or more cells high, the lobes with a uniseriate row of 1–3(4) cells, the lobes ± parallel, ± ventrally sulcate . . . . . *L. pendulina* (p. 206)

The following treatment of taxa is adapted and modified from Engel and Schuster (2001).

Subg. ***Dendrolepidozia*** R.M.Schust.

Lepidozia subg. *Dendrolepidozia* R.M.Schust., J. Hattori Bot. Lab. 36: 386. 1973 (1972). Type: *Lepidozia spinosissima* Mitt.

Lepidozia spinosissima (Hook.f. & Taylor) Mitt.

[Plate 6A, C; Fig. 29; Fig. 34: 1, oil-bodies, p. 220]

Sendtnera spinosissima Hook.f. & Taylor *in* Taylor, London J. Bot. 5: 373. 1846. *Lepidozia spinosissima* (Hook.f. & Taylor) Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 146. 1854. *Herbertia spinosissima* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 397. 1877. Type: New Zealand, *Edgerley* (*non vidi*).
Lepidozia longifissa Steph., Sp. Hepat. 6: 364. 1922. Type: New Zealand, *Zürn* (*non vidi*).

Plants erect, rigid, with somewhat ventrally secund spinescent branches, light green to yellow-brown, the shoots to 3.2 cm wide, including branches. Branching mostly of *Frullania* type, consistently 2-pinnate (rarely 3-pinnate), the branches whip-like, occasionally becoming flagelliform, the leaves like those of main shoot except smaller; branch half-leaf 2-lobed or sporadically unlobed; first branch underleaf 2–3(4)-lobed, inserted on ventral-lateral side of main axis in similar plane to leaves of the main shoot. *Acromastigum*-type branches (?)occasional. Ventral-intercalary branching occasional. Stems rigid, the cortical cells in 1 layer of thick-walled cells; medullary cells thick-walled, gradually becoming larger in diameter toward stem-middle. Leaves rigid, plane or feebly concave, approximate, 0.7–1 mm long at longest point, 0.8–1.3(1.5) mm wide at widest point, stiffly patent, the insertion narrow, transverse; leaves slightly asymmetric, subequally deeply 4(5)-lobed, divided to ca. 0.7–0.9, the lobes widely divergent, the distance from dorsal sinus-base to insertion not much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes narrowly and gradually attenuate, entire, 6–8(10) cells wide at base, terminating in a uniseriate row of (6)7–12 cells; cells of uniseriate row thick-walled, ± isodiametric to slightly longer than wide. Disc moderately asymmetric, 7–9 cells high at dorsal sinus, 3–6 cells high at ventral sinus, the margins entire, the dorsal margin straight to slightly curved. Cells of disc-middle thick-walled, trigones medium and straight-sided, isodiametric to longitudinally elongate along the lobe axis (the leaves thus subvittate), (15)18–27(32) × 26–35 μm; surface smooth. Oil-bodies in all leaf cells including uniseriate row, occupying a conspicuous portion of cell lumen, hyaline, (3)4–6 per median disc cell, moderately botryoidal, with age the spherules coalescing and the oil-bodies becoming coarsely botryoidal, elliptic to short- to long-fusiform to at times linear, some subglobose, 4 × 8 μm to 3.5–4 × 10–13 μm, spherical ones 4–5 μm in diam.; basal cells with same number per cell but larger and more coarsely botryoidal, up to 16 × 6 μm. Underleaves widely spreading, symmetrically 4-fid to ca. 0.7–0.9, the lobes ±

Fig. 29.
Lepidozia spinosissima (Hook.f. & Taylor) Mitt. 1. Plant showing androecia on primary and secondary branches, the main axis with 9 androecia from ventral face of stem between arrows a and b, the plant also with a number of androecia (not shown) between the plant base and those drawn (these basal ♂ not included appear older, at times broken and presumably from a previous year of

parallel to slightly divergent, filiform-attenuate, usually entire, rarely with a cilium toward base; disc 3–6 cells high at median sinus, the disc margins entire.

Androecia on inconspicuous, short, determinate, tightly spicate, cernuous, ventral-intercalary branches from main stem as well as primary and secondary branches or terminating on such branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.5, the lobes apiculate to short-acuminate; antheridial stalk biseriate. Gynoecia rarely produced, on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, narrowly ovate to subelliptic, shallowly and irregularly 3–4-lobed, the lobes acute to acuminate, the lobe tips composed of a uniseriate row of 2 cells or a single cell or several laterally juxtaposed cells; lamina margins composed of narrowly elongate cells somewhat irregular in shape, the cells of median and basal portion of margin not projecting, the margin distally with cells often divergent and forming a crenulation and (sporadically) the margin with a few small teeth; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth narrowing toward the contracted, shallowly lobulate mouth, the mouth crenulate-denticulate, the teeth composed of a single cell or a uniseriate row of at most 3 cells.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island, South Island (30–300 m), North Island (200–610 m), Chatham Islands. It occurs in the western, higher rainfall parts of the country, in Fiordland, Westland, Western Nelson, Southern North Island, Taranaki, Auckland and Northland EPs.

A species of dense, wet, rich, low- to middle-elevation forests (typically sea level to 365 m) dominated by a variety of canopy species such as *Weinmannia racemosa*, *W. silvicola*, *Metrosideros umbellata*, *Nothofagus menziesii*, *N. truncata* and *N. solandri*. It typically occurs over decaying organic matter, such as on the forest floor among leaf litter and to a lesser extent on old logs. When terricolous, it occurs in particularly humid niches, such as damp hollows, stream banks, moist, shaded, humus-covered banks and boggy areas. It also may occur as a component of dense bryophyte cover of vertical, dripping cliffs, such as those along the sea-level track to Bowen Falls at Milford Sound, and may extend as high as 940 m on Mt. Te Aroha (North Island), where it is on vertical cliff faces in a forest dominated by *Nothofagus menziesii* and *Griselinia littoralis*. Also known from the summit area of "Little Moehau" (Coromandel Forest Park, ca. 850 m) on soil deep in a protected pocket of a ledge of a large rocky outcrop in an area of exposed bedrock, with tufts of vegetation in protected pockets and

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growth). 2. Main shoot with androecium, ventral view (the leaf at lower left not shown); note also terminal branch and position of first branch underleaf. 3. Antheridium. 4. Portion of plant with perianth, ventral view; note primary and secondary terminal branches and the position of the first branch underleaves. 5. Innermost bracts and bracteole. 6. Bract lobes. 7. Perianth, cross sections through median sector (a), distal 0.2 (b) and near apex (c). 8. Portion of perianth mouth. 9. Two leaves and (at right) an underleaf of main axis (DS = dorsal sinus). 10. Half-leaf. 11. First branch underleaves. (Figs. 1–3, from *Braggins 98/311*, New Zealand, North Is., Northland EP, E edge of Waipoua Forest, Mataraua Plateau; 4–8, from *Cameron 3797a*, New Zealand, Auckland EP, Coromandel Ra., SW side of Maumaupaki; 9–11, from *Engel 21109*, New Zealand, North Is., Northland EP, SE corner of Waipoua Forest, just N of Tutamoe.)

crevices, and with windswept, dense scrub at the base, including *Leptospermum scoparium*, *Dracophyllum recurvum* and *Phyllocladus alpinus*. Accompanying species are: *Acromastigum colensoanum*, *Balantiopsis diplophylla*, *Bazzania adnexa*, *B. monilinervis*, *B. nitida*, *Categonium nitens*, *Distichophyllum pulchellum*, *Heteroscyphus coalitis*, *Hymenophyton flabellatum*, *Hypnodendron menziesii*, *Hypnum chrysogaster*, *Kurzia hippuroides*, *Lepidozia hirta*, *L. kirkii*, *Leucobryum candidum*, *Metzgeria leptoneura*, *Plagiochila retrospectans*, *Pyrrhobryum mnioides*, *Schistochila balfouriana*, *S. glaucescens*, *S. nobilis*, *Temnoma pulchellum*, *Trichocolea mollissima*, *Tylimanthus saccatus*, *T. tenellus* and *Zoopsis argentea*.

Comments: *Lepidozia spinosissima* is one of the most distinctive New Zealand species of the genus. The erect, wiry plants with stiffly spreading, ventrally secund, spinescent branches, and the distant, rigid, stiffly patent, transversely inserted, deeply and symmetrically divided leaves are immediately recognizable.

Subg. ***Mastigolepidozia*** R.M.Schust.

Lepidozia subg. *Mastigolepidozia* R.M.Schust., Beih. Nova Hedwigia 118: 187. 2000. Type: *Lepidozia microphylla* (Hook.) Lindenb.

Sect. ***Microphyllae*** (Lindenb.) Grolle

Lepidozia sect. *Microphyllae* (Lindenb.) Grolle, Feddes Repert. 87: 269. 1976. *Lepidozia* I. *Microphyllae* Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 201. 1845. Lectotype (*fide* Grolle, 1976): *Lepidozia microphylla* (Hook.) Lindenb.

Lepidozia microphylla (Hook.) Lindenb.

[Plate 5E, F]

Jungermannia microphylla Hook., Musci Exot. 1: *pl. 80, f. 1–6*. 1818. *Mastigophora microphylla* (Hook.) Mont. *in* d'Orbigny, Voy. Amér. Mér. 7, Bot. 2: 73. 1839. *Lepidozia microphylla* (Hook.) Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 202. 1845. Type: New Zealand, South Is., Dusky Bay, *Menzies* (2), ex Kew, ex herb. Bescherelle (G!).
Lepidozia multipinna Steph., Sp. Hepat. 3: 591. 1909. Type: New Zealand, *Dall* (G!).

Plants erect, rigid, distinctly wire-like, delicate in appearance, with drooping, ventrally secund branches, the branch axils (in field) with prominent, glistening droplets of water, the plants pale green (± straw-like color or whitish in herb.), the shoots to 4.5 cm wide, including branches. Branching mostly of *Frullania* type, consistently 2-pinnate (occasionally 3-pinnate), the branches whip-like, filiform-attenuate, the leaves scale-like, obliquely spreading, approximate; branch half-leaf often caducous; first branch underleaf 2–4-lobed, inserted on main axis in similar plane to leaves of main shoot. Ventral-intercalary branching occasional. Stems fleshy, rather brittle, the cortical cells in a distinct layer of cells larger in diameter than subepidermal cells; medullary cells thick-walled, the outer several rows with walls thicker than the median core cells. Leaves inconspicuous, scale-like, narrower than the stem, slightly concave, markedly distant, (340)385–420(450) μm long at longest point, (340)380–450(490) μm wide

at widest point, strongly erect, commonly ± appressed to stem, occasionally feebly spreading, the insertion transverse to weakly incubous; leaves asymmetric, unequally 4-lobed, divided to ca. 0.4–0.5 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes acuminate, entire, 4–5 cells wide at base, terminating in a uniseriate row of 2–4(5) cells; cells of uniseriate row ± isodiametric, thick-walled; surface as in disc. Disc asymmetric, 7–9 cells high at dorsal sinus, 3–5 cells high at ventral sinus, the margins entire, the dorsal margin straight to slightly curved. Cells of disc-middle thick-walled, ± isodiametric, 24–31 μm wide and long; surface faintly striate-papillose. Oil-bodies (Engel and Schuster, 2001) 2–5 per median cell, finely botryoidal and almost granular in aspect (the spherules small), the oil-bodies relatively large for cell size, 3.5 × 6.5 μm to, more usually, 4.5–5 × 7–11 μm. Underleaves minute, widely spreading, symmetrically quadrifid to ca. 0.3–0.4, the lobes abbreviated, only 3–5 cells long; disc 3–4(5) cells high at median sinus; disc margins entire. Fungal partner an ascomycete.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from primary or secondary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.4, the lobes acute to apiculate to short-acuminate; antheridial stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave to canaliculate, narrowly ovate; apices with 4 short, irregular lobes, the lobes crenate-denticulate to ciliate; lamina margin bordered by elongate, thin-walled, sinuate-rhomboidal cells that at their apical end occasionally diverge to form a projection, the margin irregularly crenate-denticulate to the base; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly 3-plicate toward mouth, the perianth gradually narrowing toward the contracted, shallowly 3-lobed mouth, the lobes composed of irregularly sinuate-rhomboidal cells that at the apical end are laterally free for varying lengths, the lobes crenate-denticulate to ciliate.

Capsule oblong, the wall 54–60 μm thick, of 4–5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and several small nodules alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls usually devoid of thickenings or sporadically with an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, with semiannular bands common, rather wide, close and numerous, usually complete.

Spores 10.1–11.9 μm in diam., spore wall pale brown, thin, with low, rather coarse, close papillae and short-vermiculate markings. Elaters rigid, nontortuous, 11–14.9 μm wide, only slightly tapering toward tips, bispiral, the spirals 3.4–4.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (0–600 m), North Island (280–600 m), Chatham Islands. It occurs in the western, higher rainfall parts of the country, in Fiordland, Westland, Western Nelson, Auckland and Northland EPs.

A species typically of dense, wet, rich, lower-elevation forests with canopy dominants of *Agathis australis*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Weinmannia racemosa*, *W. silvicola*, *Nothofagus menziesii* and *N. fusca*. It typically occurs on the forest floor where it may form extensive, dense carpets. It is a locally common floor plant at some sites, such as rich mixed *Nothofagus* forests or kahikatea swamps, and often occurs in boggy, seepage niches. To a lesser extent it also may be found on old logs or tree bases (such as of *Agathis australis*).

The species is also able to tolerate more rigorous sites, such as near the summit of "Little Moehau" (Coromandel Forest Park, ca. 800–840 m). Here it formed very thick mats over old wood in an area of rocky outcrops and shrub-heath communities including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus* and *Corokia buddleioides*. It may be found under *Leptospermum scoparium* scrub.

Accompanying species are: *Achrophyllum dentatum*, *Adelanthus falcatus*, *Bazzania novaezelandiae*, *Clandarium xiphophyllum*, *Distichophyllum pulchellum*, *Heteroscyphus cymbaliferus*, *Hymenophyton flabellatum*, *Hypnodendron menziesii*, *Canalohypopterygium tamariscinum*, *Isotachis montana*, *Lepidozia pendulina*, *L. spinosissima*, *Metzgeria leptoneura*, *Paraschistochila pinnatifolia*, *Plagiochila gigantea*, *Ptychomnion aciculare*, *Pyrrhobryum mnioides*, *Rhacocarpus purpurascens*, *Schistochila appendiculata*, *S. glaucescens*, *S. nobilis*, *Sphagnum australe*, *S. falcatulum*, *Telaranea tetradactyla*, *Thuidium laeviusculum*, *Trichocolea mollissima* and *Tylimanthus saccatus*.

Comments: *Lepidozia microphylla* is immediately recognizable by the erect, fleshy, pale yellow-green shoots with rigid, distinctly wire-like, drooping, ventrally secund branches. The shoots are rather brittle when dry. The leaves are inconspicuous, distant and scale-like, nearly appressed to and narrower than the stem, and almost transversely inserted. A distinctive field character of the species is the presence of tiny, glistening water droplets in the branch axils.

The stem is unique among our species of the genus in having a rather well-defined hyaloderm, surrounding a layer 1–2(3) strata thick of somewhat smaller, very thick-walled cells that gradually grade into a firm-walled medulla (Engel and Schuster, 2001, fig. 9: 14).

Subg. ***Notholepidozia*** R.M.Schust.

Lepidozia subg. *Notholepidozia* R.M.Schust. *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. 42: 31. 2001. Type: *Lepidozia novae-zelandiae* Steph.

Sect. ***Pendulinae*** R.M.Schust.

Lepidozia sect. *Pendulinae* R.M.Schust., Beih. Nova Hedwigia 118: 197. 2000. Type: *Lepidozia pendulina* (Hook.) Lindenb.

Lepidozia pendulina (Hook.) Lindenb.

[Plate 5D; Fig. 34: 2, oil-bodies, p. 220]

Jungermannia pendulina Hook., Musci Exot. 1: *pl. 60, f. 1–5*. 1818. *Lepidozia cupressina* var. *pendulina* (Hook.) Lehm. & Lindenb. *in* Lehm., Nov. Min. Cogn. Stirp. Pug. 4: 39. 1832. *Lepidozia pendulina* (Hook.) Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 208. 1845. *Mastigophora pendulina* (Hook.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. Type: New Zealand, South Is., Dusky Bay, 1791, *Menzies*, ex herb. Kew (G!).
Lepidozia gigantea Steph., Sp. Hepat. 3: 600. 1909. Type: New Zealand, *Dall "Doll"* (G!).

Plants erect, rigid, with ventrally secund branches, pale green, the shoots robust, to 6 cm

wide, including branches. Branching mostly of *Frullania* type, consistently 2-pinnate (rarely 3-pinnate), the branches whip-like, often becoming flagelliform, the leaves like those of main shoot except smaller; branch half-leaf 2-lobed or sporadically unlobed; first branch underleaf (3)4-lobed, inserted on ventral-lateral side of main axis in a plane similar to leaves of main shoot. Ventral-intercalary branching rare and sporadic. Stems rigid, the cortical cells in 1 layer of firm-walled cells, internal to the epidermal layer are 2–3 to 4–6 rows of thick-walled cells; central portion of stem made up of cells larger in diameter and with thin walls. Leaves rigid, slightly concave, distant, 1.1–1.4 mm long at longest point, (1.7)1.9–2.5 mm wide at widest point, stiffly patent, the insertion transverse; leaves asymmetric, unequally 4(6)-lobed, the leaves divided to ca. 0.65–0.75 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion. Lobes broadly attenuate (the dorsal lobes acute, the ventral lobe more narrowly attenuate and curved), the dorsal pair of lobes partially united, the others distinct and spreading, the ventral lobe often widely divergent as a "claw," the dorsal lobes entire, (10)14–24 cells wide at base, the lobes terminating in a uniseriate row of 2–4(6) cells (6–7 in ventral-most lobe); cells of uniseriate row ± isodiametric to slightly longer than wide, thick-walled. Disc distinctly asymmetric, 20–30 cells high at dorsal sinus, 12–18 cells high at ventral sinus, the margins entire, the dorsal margin broadly ampliate, the ventral slightly curved. Cells of disc-middle thick-walled, trigones medium and straight-sided, occasionally with intermediate thickenings, ± isodiametric to elongate, 18–26(29) μm wide × 24–33(42) μm long, in ± regular longitudinal files; median basal cells enlarged, in 1–2 rows, with walls often nodulose; surface smooth to indistinctly striate. Oil-bodies occupying a small portion of cell lumen, hyaline, (2)3–4(5) per cell at base of dorsal sinus (in median cells (2)3–8 per median cell, locally to 10–14 per cell, *fide* Engel and Schuster, 2001), globose to elliptic to fusiform, a few linear in profile, botryoidal, but quickly breaking up by becoming increasingly botryoidal via swelling of spherules, 4.3–4.8 × 7.7–8.6 μm to 4.3–6.2 × 10.6–12.5 μm, globose ones 4.3–4.8 μm in diam. Underleaves often weakly to distinctly plicate, widely spreading, symmetrically 4(6)-fid to ca. 0.65–0.7 (median sinus), the sinus bases somewhat reflexed, the lobes ± parallel, somewhat ventrally sulcate, narrowly and gradually attenuate, entire, terminating in a uniseriate row of 1–3(4) cells; disc margins reflexed, entire or sporadically with a tooth. Fungal partner an ascomycete.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches from main shoot and primary + secondary branches (in flagelliform or leafy sectors); bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes acute to short-acuminate; antheridial stalk biseriate. Gynoecia only sporadically produced, on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, broadly ovate-subrectangular; apices with 4–5 short, ± regular lobes, the lobes finely crenulate; lamina margin bordered by thin-walled cells of variable shape and orientation, the cells often ± sinuate-rhomboidal, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenulate to crenate-denticulate; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobe margins composed of irregularly sinuate-rhomboidal cells that, at the apical end, project for varying lengths, the mouth thus crenate-denticulate.

Seta with 16 rows of outer cells surrounding an inner core of numerous much smaller cells. Mature capsules not seen.

Distribution and Ecology: New Zealand: Stewart Island (5 m), South Island (0–1200 m), North Island (1000–1200 m); Australia: Tasmania, Victoria. Occurs in mainly western, high rainfall parts of the country but extends to the centers of both main islands. Found in Fiordland, Southland, Westland, western edges of Canterbury, Western Nelson, Southern North Island (Tararua and Ruahine ranges), Taranaki (Egmont Natl. Park), Volcanic Plateau (Tongariro Natl. Park) and Gisborne (Urewera Natl. Park) EPs. Apparently absent from Auckland and Northland provinces.

The species occurs in dense, very wet to only moderately wet forests over a broad altitudinal gradient, but is more typical of middle- to upper-elevation sites. It occurs in *Nothofagus solandri*, *N. menziesii* and *N. truncata* forest. Other species such as *Metrosideros umbellata* and *Weinmannia racemosa* may also be present as canopy species, but *Lepidozia pendulina* seems to be confined to forests in which *Nothofagus* is present. For example, it may occur at the upper limits of *N. menziesii* forests (stations at ca. 900 m in the South Island, and ca. 1180 m in the North Island) as well as in upper montane *N. solandri* forests with *Phyllocladus alpinus*, *Brachyglottis buchananii*, *Pseudopanax* spp., *Dracophyllum traversii* and *Coprosma*. In the southern sectors of South Island it occurs in forests at lower elevations including at sea level.

The species typically occurs over organic substrates such as the forest floor (particularly in damp leaf litter) where it may form extensive, at times large, pure carpets that at times raise to low-lying mounds; it may be associated with *Bazzania nitida*, *Lepidogyna hodgsoniae*, *Plagiochila gigantea*, *Schistochila nobilis* and *Trichocolea mollissima*. It also occurs on damp, bryophyte-covered banks and wet, bryophyte-covered, rotted logs. The species often is a component of the flora of sites where the floor, boulders and trees are densely covered with bryophytes. Associated species are: *Adelanthus falcatus*, *Bazzania adnexa*, *Blepharidophyllum vertebrale*, *Breutelia pendula*, *Chiloscyphus mittenianus*, *Cryptochila grandiflora*, *Dendroligotrichum dendroides*, *Dicranoloma billardierei*, *D. robustum*, *Gackstroemia weindorferi*, *Herbertus oldfieldianus*, *Heteroscyphus cymbaliferus*, *H. sinuosus*, *Hymenophyllum multifidum*, *Lepidogyna hodgsoniae*, *Leptotheca gaudichaudii*, *Paraschistochila pinnatifolia*, *Plagiochila gigantea*, *P. retrospectans*, *Pogonatum subulatum*, *Pseudocyphellaria multifida*, *Ptychomnion aciculare*, *Pyrrhobryum bifarium*, *Rhizogonium distichum*, *Schistochila appendiculata*, *S. ciliata*, *S. glaucescens*, *S. nobilis*, *Trichocolea mollissima*, *Tylimanthus saccatus* and *Wijkia extenuata.*

Comments: Well-developed plants of this species are not likely to be confused with any other New Zealand member of the genus on general aspect alone. Distinctive are the bipinnate branching (small, poorly developed populations have secondary branches weakly developed or absent); the broad, transversely inserted, entire-margined leaves; the large underleaves with ± parallel, ventrally sulcate lobes; and the leaf areolation, the leaf cells thick-walled, arranged in ± regular longitudinal files, and appearing small and narrow in proportion to the size of the leaf, giving the leaf a densely cellular appearance, even under the dissecting microscope.

Sect. ***Setigerae*** R.M.Schust.

Lepidozia sect. *Setigerae* R.M.Schust., Beih. Nova Hedwigia 118: 193. 2000. Type: *Lepidozia setigera* Steph.

Lepidozia setigera Steph.

[Fig. 34: 3, oil-bodies, p. 220]

Lepidozia setigera Steph., Sp. Hepat. 3: 599. 1909. Type: New Zealand, South Is., Okarito, *Kirk 590* (G!).

Plants suberect to loosely ascending, somewhat flexuous, with ventrally secund branches, pale green, the shoots robust, to 3 cm wide, including branches. Branching mostly of *Frullania* type, closely and regularly pinnate, the primary branches often very long, becoming whip-like and flagelliform, the primary branches occasionally developing into new leading shoots; secondary branches occasionally present, 1(2) per primary branch; branch half-leaf ± symmetric, broadly ovate, 2-lobed to ca. 0.5, entire; first branch underleaf 3–4-lobed, with a few marginal cilia, inserted on lateral side of stem immediately below branch base and aligned with leaves of main shoot. Ventral-intercalary branching sporadic, stoloniform or leafy and developing into a new leading shoot. Stems stiff and woody, the cortical cells in 1 layer of thin-walled cells distinctly larger than medullary cells (up to 2× larger); medullary cells moderately thickened, the outer several rows with walls thicker than the median core cells. Leaves rigid, slightly concave, strongly imbricate and completely hiding stem in dorsal view, 1.5–1.7 mm long at longest point, 2–2.4 wide at widest point, patent, the insertion distinctly incubous and somewhat recurved at dorsal end; leaves distinctly asymmetric, unequally 4(5)-lobed, the leaves divided to ca. 0.5–0.6 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, gradually becoming deeper ventrally. Lobes subulate, the ventral lobe often spreading as a "claw," the lobes entire, the dorsal lobes 8–11 cells wide at base, terminating in a uniseriate row of 6–10(12) cells (the ventral often somewhat longer); cells of uniseriate row often hyaline, tapering, with ± swollen dilated septa, 2–5:1, thick-walled, becoming longer and narrower toward the tip and capillary, the terminal cells finely tapering, 8–10:1, the surface finely striate-papillose. Disc distinctly asymmetric primarily due to strong dilation of dorsal sector, the dilated portion up to ca. 0.5 the disc area, the disc (18)20–25 cells high at dorsal sinus, 12–16 cells high at ventral sinus; dorsal margin distinctly and broadly ampliate, entire. Cells of disc-middle thin-walled, trigones large and bulging to knot-like, 26–33 μm wide × 34–52 μm long; median basal cells larger; surface smooth to indistinctly striate-papillose. Oil-bodies hyaline, 8–12 per cell in upper disc, subglobose to broadly to narrowly elliptic to ± linear, finely botryoidal, the spherules rather soon swelling. Underleaves often distinctly connate on one side (the connation to 7–8 cells high), spreading, concave, imbricate, symmetrically 4-fid to ca. 0.5–0.6 (median sinus), the sinus bases somewhat reflexed, the lobes plane or reflexed, diverging, filiform-attenuate from a narrow base and ultimately with a long-ciliiform tip, entire or with a ciliiform spine, the lobes appearing to terminate in a blunt tip, the lobe continuing as a subapical, often abaxially oriented, ciliiform process with a uniseriate row of 8–13 cells; disc margins somewhat reflexed, on each side often with a ciliiform process distally, the underleaves then appearing 6-lobed.

Androecia not seen. Gynoecia rarely produced, on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, broadly ovate to suborbicular from a narrow base, 4(6)-lobed to ca. 0.5–0.6, the lobes caudate, the setaceous tips composed of a uniseriate row of 6–10, thick-walled, elongate cells, the lobes entire or with a few short to long basal cilia; lamina margins armed with spinose teeth and straight to contorted cilia; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous in distal 0.25–0.4, distinctly and deeply triplicate toward mouth, the perianth gradually narrowing toward the strongly contracted, contorted mouth, the contracted sector membranous and, with emergence of the capsule, splitting into 4–6 narrowly long-attenuate lobes; mouth cells 4–9:1, laterally fused for varying lengths and thickened at the summit, the mouth thus rather regularly crenulate to crenate-denticulate.

Seta 30–40 mm long, with 12–13 rows of large outer cells surrounding an inner core of ca. 40–50 small cells. Capsule wall 52–54 μm thick, of 5–6 layers; outer layer of cells with two-phase development, the longitudinal walls very thin, with sinuous, sheet-like swellings and a few nodule-like swellings alternating with walls that are devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically have an isolated sheet-like thickening; innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, narrow, close and numerous, sporadically incomplete.

Spores 11–12.5 μm in diam., spore wall brown, thin, with dense, close papillae and short-vermiculate markings. Elaters rigid, nontortuous, 15.8–16.8 μm wide, slightly tapering toward tips, bispiral, the spirals 4.8–5.3 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (60–305 m), North Island (260–340 m). Occurs in Southland (Catlins), Westland, Western Nelson, Auckland (Great Barrier Island) and Northland EPs. Not known from Fiordland or Stewart Island.

The species occurs sporadically in lowland forests where it is terricolous (at times forming small mounds) or on old, humus-covered logs, at times mixed with *Bazzania adnexa*. In the North Island it chiefly occurs in *Agathis* forests. It is rather common in the Waipoua Forest Reserve on relatively well-insolated peaty ground under, for example, old *Leptospermum scoparium* or on very rotted, bryophyte-covered shaded logs (at times mixed with *Schistochila glaucescens*) in *Agathis* forest containing *Dacrydium* and other podocarps.

Also known from *Dacrydium cupressinum – Nothofagus menziesii* and *N. fusca* forests, and from *Leptospermum scoparium* scrub. Found with *Acromastigum anisostomum*, *Bazzania novae-zelandiae*, *Lepidozia microphylla*, *Rhaphidorrhynchium amoenum*, *Schistochila balfouriana* and *Tylimanthus saccatus*.

Comments: This is one of the easiest of our species to identify. The lobes of both leaves and underleaves are setaceous at their apices, terminating in a uniseriate row of greatly elongated cells (8–10:1). Unlike *Lepidozia ulothrix*, which also has lobes terminating in a uniseriate row of elongated cells, this species has disc and lobe margins that are uniformly entire. Also notable is the broad and marked ampliation of the dorsal sector of the leaf, the dilated portion up to half of the disc area.

Sect. ***Notholepidozia***

Lepidozia procera Mitt.

[Fig. 30]

Lepidozia procera Mitt. *in* Hook.f., Bot. Antarc. Voy. 3: 231. *pl. 180, f. 1*. 1859. Type: Tasmania, without specific locality, *Gunn*; Mt. Wellington, *Oldfield* (*non vidi*).

Lepidozia breviloba Steph., Sp. Hepat. 3: 596. 1909. Type: New Zealand, Great Barrier Is., *Kirk* (*non vidi*).

Plants erect, slender and wiry, with strongly ventrally secund branches that are often oriented parallel with one another, pale green, the shoots to 1.5 cm wide (stem to branch extremities). Branching nearly exclusively of *Frullania* type, closely and regularly pinnate, the primary branches becoming distinctly whip-like, long-flagelliform, microphyllous and rhizoidous; secondary branches rare; branch half-leaf ± symmetric, narrowly ovate, shallowly bilobed; first branch underleaf (2)3–4-lobed, inserted on ventral-lateral side of junction of main axis and branch and aligned with branch underleaves. Ventral-intercalary branching sporadic, leafy. Stems stiff, the cortical cells in 1 layer of somewhat thick-walled cells somewhat larger than the medullary cells; 1–2 subepidermal layers with walls thicker than both epidermis and internal medullary cells, the medullary cells toward stem-middle thick-walled and with trigone-like thickenings. Leaves appressed to stem at least in basal sector, somewhat concave, contiguous to weakly imbricate, 0.35–0.5 mm long and wide at longest and widest points, suberect, ventrally secund particularly when dry, the insertion weakly to distinctly incubous; leaves slightly to rather markedly asymmetric, ± equally or, more often, unequally 4-lobed, divided to ca. 0.3–0.45 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion (often markedly so). Lobes parallel to slightly divergent, short-attenuate to acute, entire, the 2 median lobes wider and often slightly longer than the outer lobes, 5–7 cells wide at base; lobes terminating in a single cell or a uniseriate row of 2–3(4) cells, the cells of uniseriate row ± isodiametric, thick-walled and with the septum distinctly thickened and swollen; surface of lobes smooth to indistinctly and obscurely papillose. Disc moderately to distinctly asymmetric, subquadrate to deltoid, 17–26 cells high at dorsal sinus, 10–16 cells high at ventral sinus, the margins entire but the septa of marginal cells distinctly thickened and swollen, the dorsal margin slightly to moderately ampliate and broadly curved, the ventral margin straight or slightly curved. Cells of disc-middle evenly thick-walled, 10–13 μm wide × 13–19 μm long, in ± regular longitudinal files; median basal cells larger (up to 2× diam. of cells of second row), in one row; surface of disc smooth. Underleaves often narrowly connate on one side, small, ca. 0.7–0.9× the stem width, ± appressed to slightly spreading, quadrate, symmetrically quadrifid to ca. 0.3–0.4, the lobes abbreviated, only (4)5–6(8) cells long; disc (5)7–9 cells high at median sinus; disc margins entire.

Androecia and gynoecia not seen.

Distribution and Ecology: New Zealand: Stewart Island, South Island (at most 200 m), North Island (200–290 m); Australia: Tasmania, Victoria, Queensland. In New Zealand known from Rakiura (Patersons Inlet), Fiordland, Otago, Westland, Western Nelson, Southern North Island, Auckland and Northland EPs.

Within New Zealand the species sporadically occurs terricolous or saxicolous in low-elevation forests in the South Island, and is known from only a few stations in the North Is-

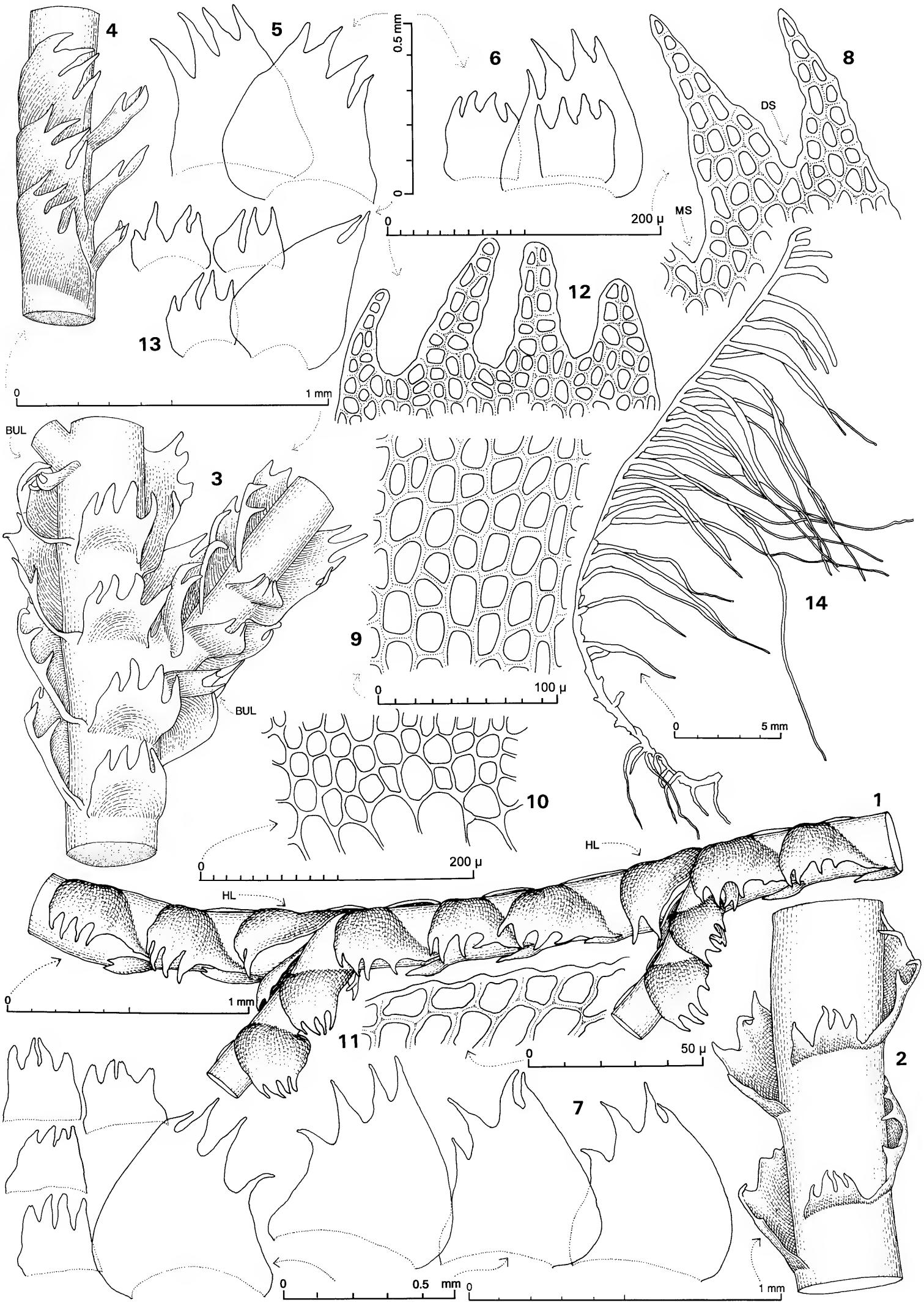

Fig. 30.
Lepidozia procera Mitt. 1. Portion of main shoot with 2 *Frullania*-type branches (HL = half-leaf), lateral view. 2. Portion of main shoot, ventral view. 3. Sector of main shoot and *Frullania*-type branch, ventral view (BUL = first branch underleaf). 4. Sector of main shoot, lateral view. 5.

land. It occurs on mossy banks in *Nothofagus* forests in Fiordland, as well over rock in a creek bed within a podocarp-dominated forest (Lake Gault, south Westland). At Waipoua Forest the species occurred over a layer of soil over a huge streambed boulder in a shaded, humid, steep-sided stream valley within a forest mainly of *Agathis australis*.

Comments: This is a distinctive species. The primary branches of *Lepidozia procera* are noteworthy in being strongly ventrally secund and often oriented parallel with one another (Fig. 30: 1, 14). The leaves are closely appressed to the stem (Fig. 30: 1, 4), and, coupled with being ventrally secund, lend the shoots and branches a markedly smooth aspect dorsally. The leaves are shallowly lobed, the two median lobes larger and somewhat longer than the outer lobes (Fig. 30: 5–7). The dorsal margin of the leaf is broadly curved and is longer than the slightly curved or straight ventral margin (Fig. 30: 5–7). The leaf areolation is also distinctive. Disc cells are evenly very thick-walled, and the cells are in longitudinal files (Fig. 30: 9). The septa of marginal cells, especially those of the dorsal margin, are distinctly thickened and swollen (Fig. 30: 11). However, this character is not always fully expressed in suboptimal populations, and several leaves should be carefully examined.

Lepidozia obtusiloba Steph.

[Figs. 31–33; Fig. 34: 4, oil-bodies, p. 220]

Lepidozia obtusiloba Steph., Sp. Hepat. 3: 598. 1909. Type: New Zealand, South Is., *Helms, Beckett* (possible isosyntypes: *Beckett 301*, Otira Gorge, 11 Feb. 1903, CHR 585840 ex herb. Beckett!; *Beckett 348*, Otira Gorge, 11 Feb. 1903, CHR 585841 ex herb. Beckett!).

Lepidozia parvitexta Steph., Sp. Hepat. 3: 598. 1909, *syn. fide* Engel and Schuster (2001). Lectotype (*fide* Engel and Schuster, 2001): New Zealand, Jacksons, *Goebel* (G! – *c. sporo.*).

Plants typically erect, rather flexuous, with laxly spreading (var. *parvula*) to strongly ventrally secund branches that are often parallel with one another, brown to yellow-brown, the shoots small to medium, to 1 cm wide, including branches. Branching nearly exclusively of *Frullania* type, rather short, closely and regularly 1(2)-pinnate, the primary branches sporadically becoming whip-like, flagelliform and microphyllous; branch half-leaf symmetrical, cordate, 2-lobed to ca. 0.2–0.4; first branch underleaf 2–3(4)-lobed, inserted on ventral-lateral side of juncture of main axis and branch and aligned with underleaves of branch or leaves of main shoot. Ventral-intercalary branching occasional, leafy or long-stoloniform. Leaves rigid, brittle, somewhat concave, imbricate and nearly or completely obscuring stem in dorsal view, 0.65–1 mm long at longest point, 0.5–1.2 mm wide at widest point (0.5–0.7 mm wide × 0.7 mm long in var. *parvula*), spreading, the insertion narrow to broad, and weakly incubous; leaves distinctly asymmetric, unequally 4(5)-lobed, the leaves divided to ca. 0.45–0.65

Leaves. 6. Leaf and 2 underleaves, at left and within leaf. 7. Four leaves and, at left, underleaves. 8. Dorsal-most 2 lobes of leaf (DS = dorsal sinus, MS = median sinus). 9. Median disc cells. 10. Median-basal cells of leaf showing row of enlarged cells. 11. Cells of dorsal margin of disc. 12. Distal sector of underleaf. 13. Half-leaf (right) and first branch underleaves. 14. Outline of plant at low magnification, lateral view. (Figs. 1, 2, 7, 11, from *Engel 21722*, New Zealand, South Is., Westland EP, Westland Natl. Park, track to Lake Gault; remainder from *Hatcher 1476*, New Zealand, South Is., Fiordland EP, head of Lake McKerrow.)

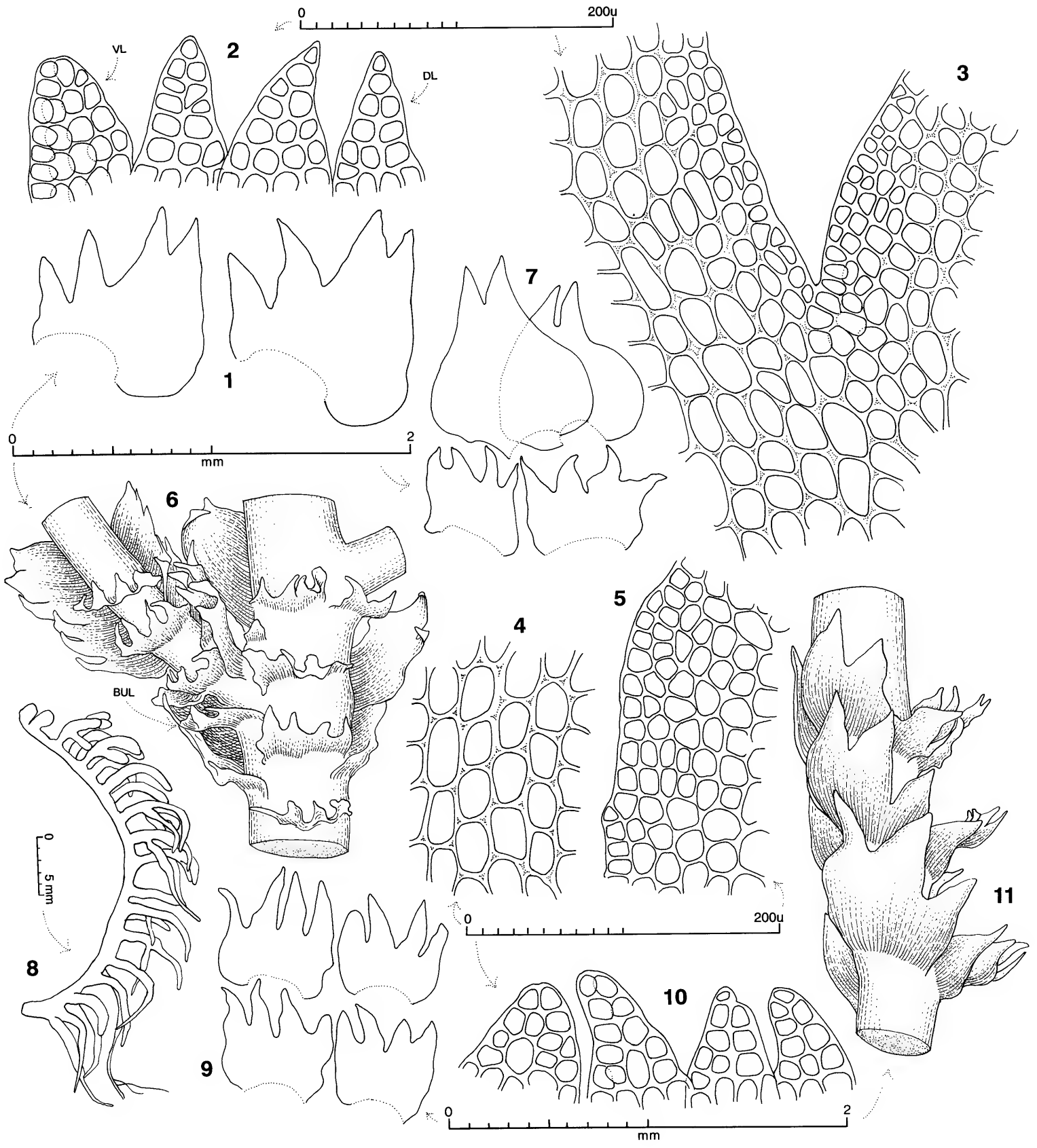

Fig. 31.
Lepidozia obtusiloba Steph. 1. Leaves. 2. Apical sectors of 4 lobes from same leaf (VL = ventral lobe; DL = dorsal lobe). 3. Base of median sinus of leaf showing border of smaller cells. 4. Median disc cells. 5. Sector of ventral margin of leaf disc showing border of smaller cells. 6. Sector of main shoot with 2 *Frullania*-type branches, ventral view (BUL = first branch underleaf). 7. Half-leaves and, below, 2 first branch underleaves. 8. Outline of shoot at low magnification, lateral view. 9. Underleaves. 10. Apical sectors of 4 lobes from same underleaf. 11. Sector of main shoot, lateral view. (All from *Engel 17843*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, off track to Mt. Brewster.)

(median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion, the dorsal sinus at times reduced to a mere notch. Lobes acute to subapiculate, the 2 dorsal lobes paired, the 2 ventral lobes widely divergent from the united dorsal lobes; dorsal lobes terminating in several laterally juxtaposed cells or a single cell or a uniseriate row of 2–3(4) cells, the cells of uniseriate row ± isodiametric, thick-walled; dorsal lobes entire, 6–8(10) cells wide at base. Disc distinctly asymmetric, 17–21 cells high at dorsal sinus, 6–10 cells high at ventral sinus, the margins entire, the dorsal margin broadly ampliate, cordate at the base, the ventral subcordate. Cells of ventral margin and lobes ± isodiametric, forming border. Cells of disc-middle thick-walled, often distinctly so, trigones sometimes present, medium and straight-sided to large and bulging, 19–28 μm wide × 24–35(42) μm long; median basal cells enlarged, in a single row; surface smooth to indistinctly striate to distinctly papillose. Oil-bodies (var. *parvula*) hyaline, (2)3–4(5) per median disc cell, subglobose to elliptic to fusiform to crescentic, distinctly botryoidal, the spherules protruding beyond membrane. Chloroplasts tiny. Underleaves widely spreading to squarrose, symmetrically 4-fid to ca. 0.4–0.55 (median sinus), the lobes plane to slightly ventrally sulcate, the sinus bases plane to slightly reflexed, the lobes short-attenuate, entire, blunt at the tip and terminating in several laterally juxtaposed cells, or with a uniseriate row of 2–3 cells; disc 7–10 cells high at median sinus, the margins parallel, plane, subcordate at base, entire or with a blunt tooth.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, often cernuous ventral-intercalary branches from main shoot; bracts ventricose-cucullate, 2–3-lobed to ca. 0.2–0.3, the lobes acute, often apiculate; antheridial stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, broadly ovate to suborbicular; apices with 4 abbreviated lobes basically smooth and only exceptionally with a crenulation, the lobe summit composed of 2 or more laterally juxtaposed cells, with each lobe terminating in a slime papilla, the lobes at times obsolete, with each represented solely by a slime papilla mounted on 2 laterally juxtaposed cells that project slightly more than neighboring cells; lamina margin bordered by thin-walled cells of variable shape and orientation, some hardly longer than wide, others ± rhomboidal, the apical or free end of marginal cells usually only sporadically divergent and forming a crenulation, the margins basically smooth except for sporadic crenulations or a several-celled tooth, or, occasionally, the margin crenulate-denticulate by variously projecting cells; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth; mouth cells laterally fused to the summit or nearly so, the mouth thus rather regularly crenulate.

Seta with 16 rows of outer cells surrounding an inner core of ca. 60 much smaller cells. Capsule long-ellipsoidal, the wall 46–48 μm thick, of 4–5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and several large nodules and spines alternating with walls that are devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically with an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete.

Spores 13.5–14.9 μm in diam., the wall brown, thin, with dense, sharply defined, close papillae and short-vermiculate markings. Elaters rigid, nontortuous, 9.6–10.1 μm wide, slightly tapering toward tips, bispiral, the spirals 3.4 μm wide.

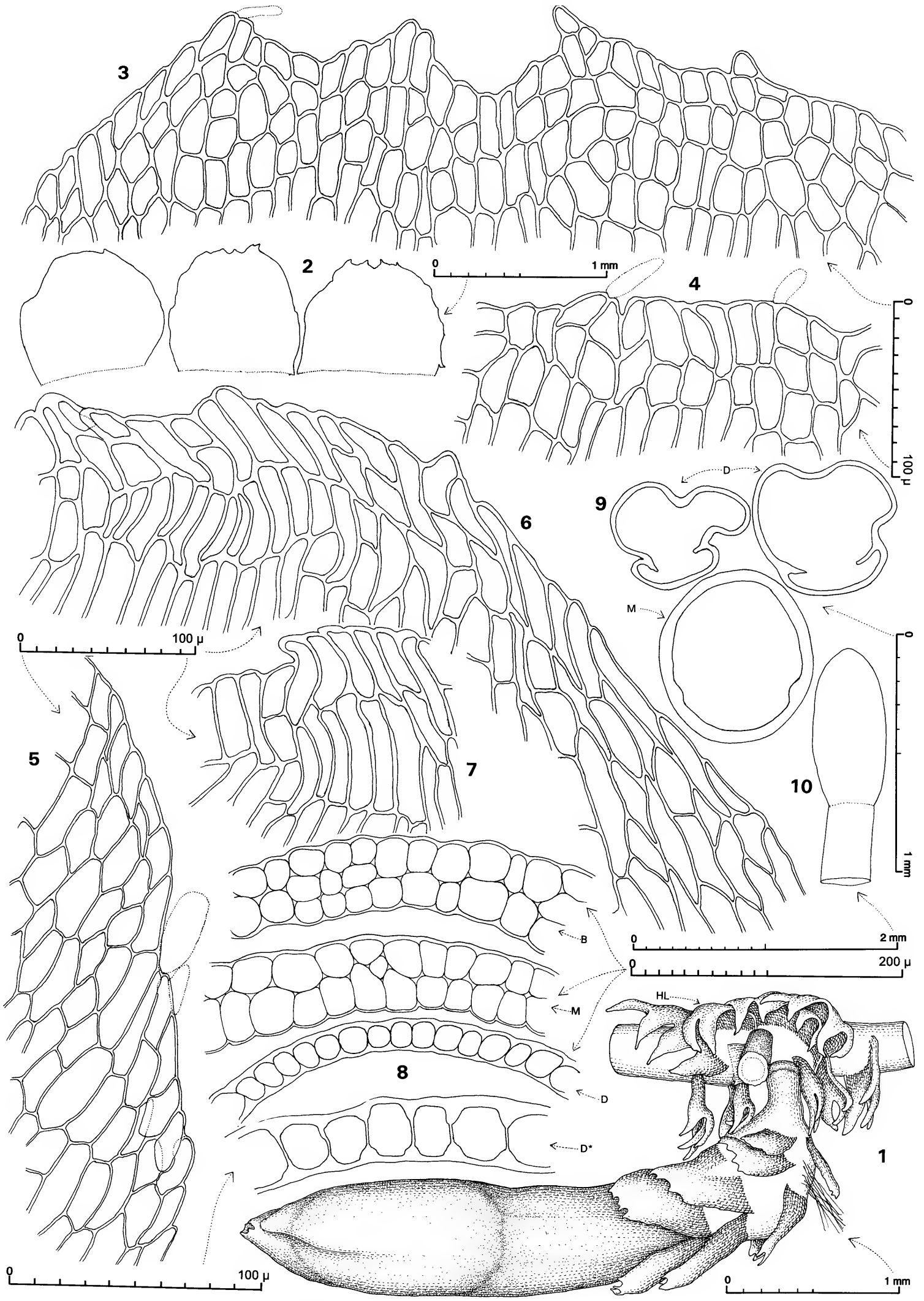

Fig. 32.
Lepidozia obtusiloba Steph. 1. Portion of main shoot with mature gynoecium; base of terminal branch shown, but with initial leaves and underleaves removed from branch for clarity (HL = half-leaf), lateral view. 2. Innermost bracts and bracteole. 3. Apex of innermost bract. 4. Portion of apex of innermost ♀ bract showing obsolete median pair of teeth, each represented by a slime papilla. 5.

Comments: The typical form of the species is distinctive because of brownish pigmentation and erect shoots with distinctly ventrally secund branches (Fig. 31: 8). The species is allied to *Lepidozia ornata*, but differs in the lack of accessory ornamentation, the broadly acute, united dorsal lobes with a shallow dorsal sinus (in *L. ornata* the lobes are narrowly acute to attenuate and narrowing to a sharp apex), and the essentially plane and unornamented underleaves. Also, the depth of the median sinus tends not to be as great as in *L. ornata*, and the ventral lobes tend to be broader than in that species. The underleaf lobes are often bluntly rounded at the summit (Fig. 31: 10), giving rise to the name.

The species has two varieties, separable as follows:

Key to Varieties

1a. Plants medium (to 1 cm wide, including branches), erect, dark brown; branches strongly ventrally secund; leaves rather broadly inserted, (0.7)0.8–1.2 mm wide × 0.65–1 mm long . . . . . var. *obtusiloba* (p. 217)

1b. Plants small (similar to *L. concinna* in size or smaller), procumbent, brown, yellow-brown to greenish; branches spreading and not distinctly secund; leaves narrowly inserted, easily detached, only 0.5–0.7 mm wide × 0.7 mm long . . . . . var. *parvula* (p. 219)

Lepidozia obtusiloba Steph. var. ***obtusiloba***

Plants medium (to 1 cm wide, including branches), erect, dark brown; branches strongly ventrally secund; leaves rather broadly inserted, (0.7)0.8–1.2 mm wide × 0.65–1 mm long.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, South Island (600–1200 m); Australia: Victoria. In New Zealand known from Fiordland (eastern ranges only), Southland (Catlins), Otago (Otago Coast, Waikaia and Lakes ERs), Canterbury (Mt. Cook Natl. Park, Upper Godley River, Upper Rakaia River, Arthur's Pass, Craigieburn Ra.), Westland (Haast Pass, Franz Josef Glacier, Otira, Kelly Ra., Nelson Lewis Pass, Lakes Natl. Park), Western Nelson (Arthur Ra.) and Sounds–Nelson (Richmond Ra., Mt. Robertson) EPs. Common east of the Main Divide, but uncommonly collected in central and south Westland or Fiordland, reflecting a preference for districts with only moderate rainfall.

A montane variety typically present in the upper reaches of forests of, mainly, *Nothofagus menziesii* or *N. solandri* forests but also found under *Libocedrus bidwillii – Griselinia littoralis – Podocarpus hallii* forest. It is often abundant, and then appears as the most common hepatic on the forest floor, on rotting logs and on tree trunks. It may form large masses on the ground and cover enormous areas (e.g., in *N. menziesii* forest at 1350 m on Mt. Arthur, Kahurangi Natl. Park). Variety *obtusiloba* may extend to the penalpine and alpine zones in protected niches on the faces of boulders or cliffs.

Portion of lateral margin of innermost bract showing nearly entire condition. 6. Perianth mouth, the summit at upper left. 7. Portion of perianth mouth. 8. Perianth, cross sections (top to bottom) through basal (= B), median (= M) and distal (= D) sectors; D* drawn at higher magnification. 9. Perianth, cross sections through median (= M) and distal portions (= D). 10. Capsule profile. (All from *Engel 17565*, New Zealand, South Is., Otago EP, S side of Mt. Cargill.)

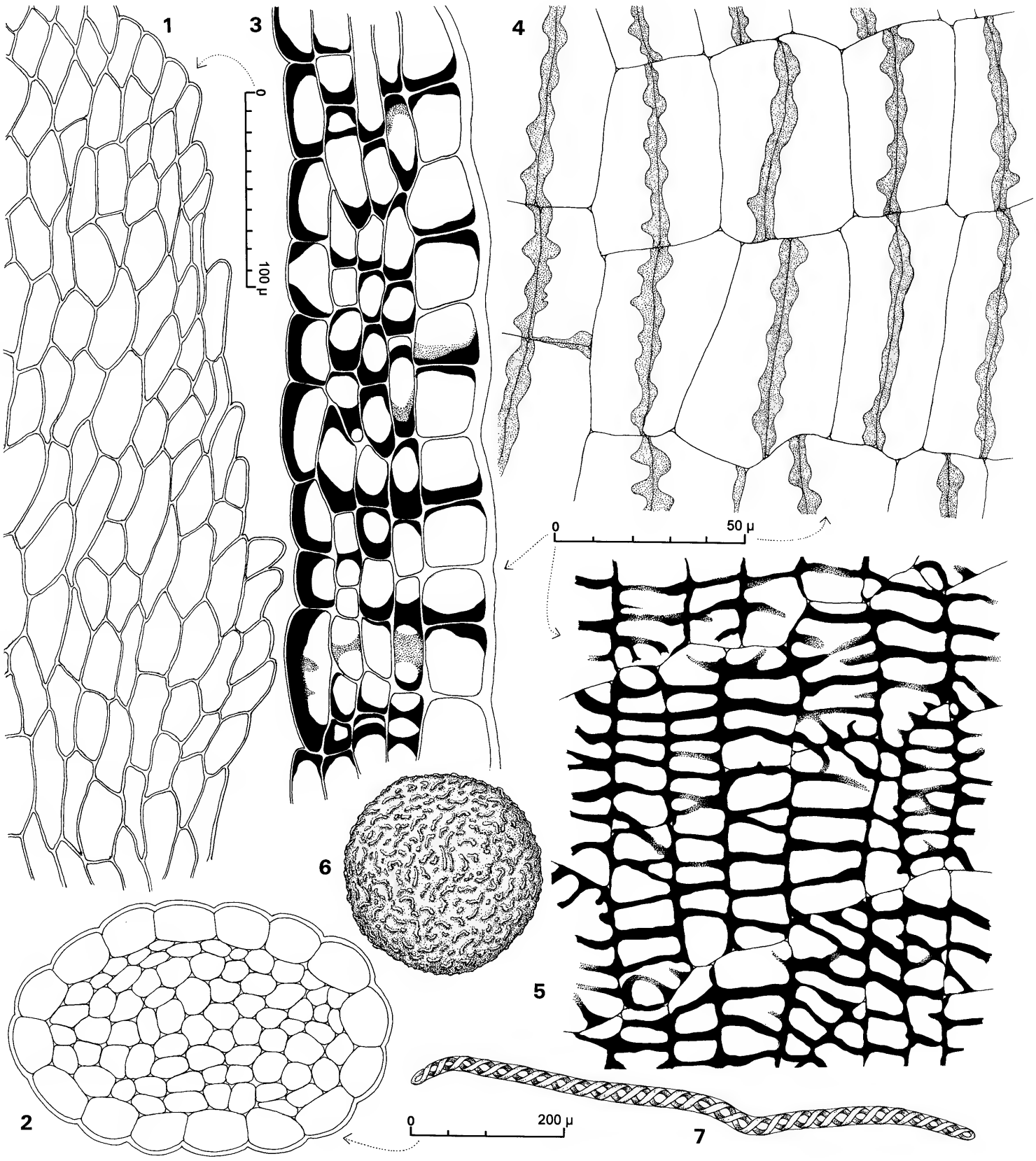

Fig. 33.
Lepidozia obtusiloba Steph. 1. Portion of lateral margin of innermost ♀ bract showing crenulate-denticulate condition. 2. Seta, cross section. 3. Capsule wall, cross section. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. 6. Spore (× 1652). 7. Elater (× 209). (All from *Engel 17565*, New Zealand, South Is., Otago EP, S side of Mt. Cargill.)

Lepidozia obtusiloba var. ***parvula*** J.J.Engel

[Fig. 34: 4, oil-bodies, p. 220]

Lepidozia obtusiloba var. *parvula* J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 48. 2001. Holotype: New Zealand, South Is., Westland Prov., Arthur's Pass Natl. Park, Kelly Ra., vicinity of Carroll Hut, above Kellys Creek, N of Otira, 1150 m, *Engel 18382* (F); isotype: (CHR).

Plants small (similar to *Lepidozia concinna* in size or smaller), procumbent to (exceptionally) suberect, brown, yellow-brown to greenish; branches spreading and not distinctly secund; leaves narrowly inserted, easily detached, 0.5–0.7 mm wide × 0.7 mm long.

Distribution and Ecology: Endemic to New Zealand: South Island (135–1400 m), North Island (1100–1270 m). Known from Southland, Otago, Westland, Canterbury (Sealy Ra., Arthur's Pass), Sounds–Nelson, Southern North Island and Gisborne (Urewera Natl. Park) EPs.

The var. *parvula* typically occurs in rock crevices or damp to dripping, often shaded, rock faces in alpine or penalpine sites (in the latter case, particularly under shrub cover, and here sporadically terrestrial). It also may occur in very wet niches, such as at the edges of tarns between tussock and covered by a layer of old tussock blades. On vertical banks of alpine rills it may form very tight compact populations with little more than the tips of each shoot exposed. The variety also (sporadically) occurs in upper-elevation forests of *Nothofagus menziesii* or *N. solandri* var. *cliffortioides* and only rarely at median or lower elevations.

Comments: Plants assigned to the var. *parvula* have an appearance quite distinct from more typical, well-developed plants of the species, being typically procumbent, with branches spreading and not distinctly secund. The leaves are smaller than in var. *obtusiloba*, more narrowly inserted and easily detached, and have disc cells often more strongly thick-walled. The color varies from brown to pale yellowish brown to greenish. They share with the typical form a brownish pigmentation, similarly shaped (though smaller) leaves, and shallowly lobed, widely spreading to squarrose underleaves.

The variety may be distinguished from *Lepidozia concinna* by the presence of brown pigments, or (when greenish) by the shorter, broader underleaf lobes, the distinctly asymmetrical leaves with a shallow dorsal sinus (which may be reduced to a mere notch) and the smaller, thick-walled median disc cells. It differs from *L. laevifolia* by the larger shoot size, the presence of brown pigments, and the imbricate, strongly asymmetric leaves that are not distinctly cup-shaped when dry.

Lepidozia ornata J.J.Engel

[Fig. 34: 5, oil-bodies, p. 220; Fig. 35]

Lepidozia ornata J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 49. *f. 17*. 2001. Holotype: New Zealand, South Is., Westland Prov., Mt. Aspiring Natl. Park, below and W of Mt. Armstrong, SSW of Mt. Brewster, ca. 1250–1450 m, *Engel 17789* (F); isotype: (CHR).

Plants suberect, stiff and wiry, rather flexuous, with spreading to weakly ventrally secund branches, warm brownish, the shoots medium, to 2.4 cm wide, including branches. Branching nearly exclusively of *Frullania* type, rather short, the pattern variable: distantly and irregularly to regularly 1(2)-pinnate, the primary branches sometimes becoming whip-like, flagelliform

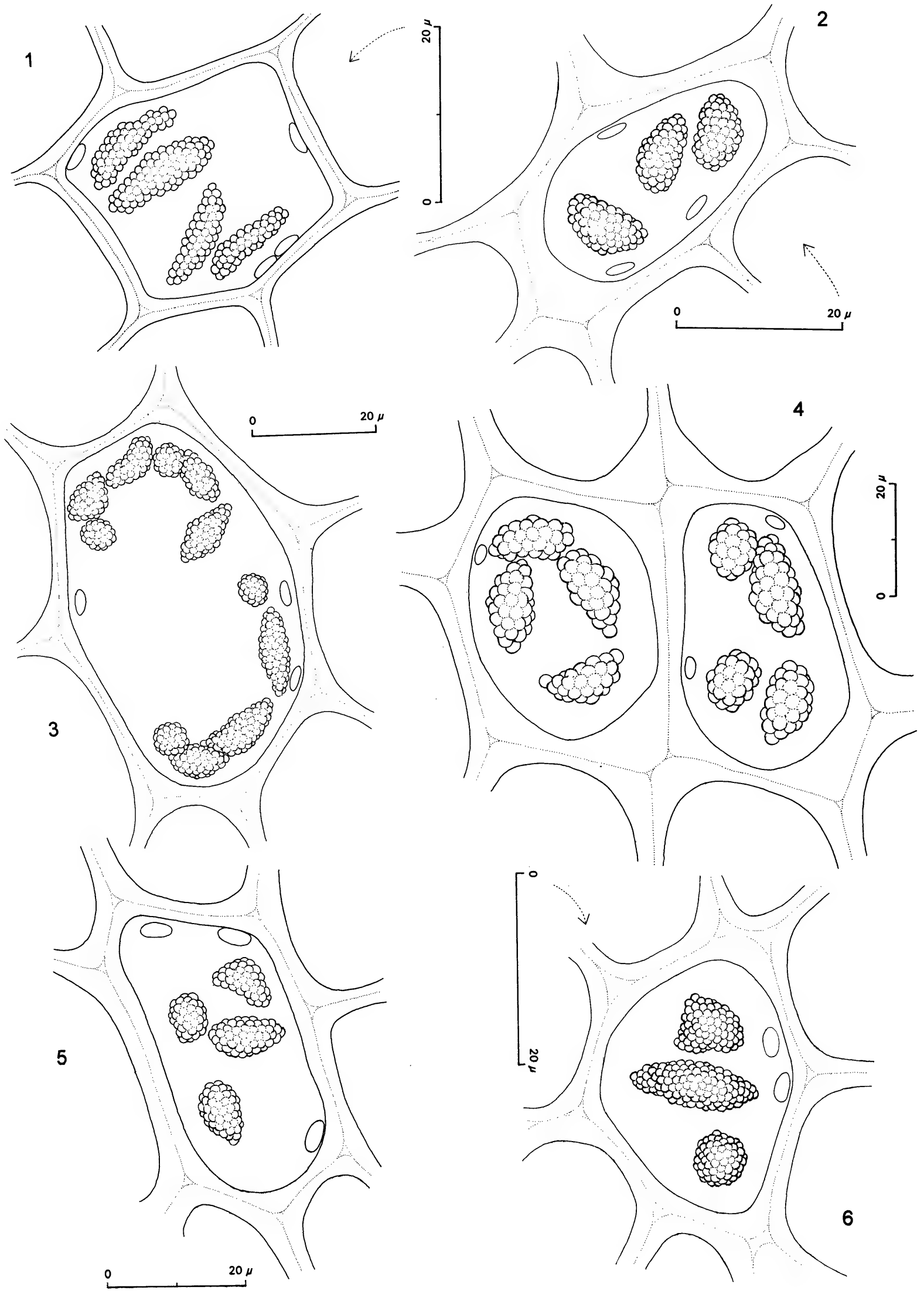

Fig. 34.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Lepidozia spinosissima* (Hook.f. & Taylor) Mitt. Basal cell of lobe. 2. *Lepidozia pendulina* (Hook.) Lindenb. Basal cell of lobe. 3.

and microphyllous; branch half-leaf subsymmetrical, cordate, 2-lobed to ca. 0.3, the base variously armed with teeth and accessory appendages; first branch underleaf 2–4-lobed, inserted on main axis or ventral-lateral side of juncture of main axis and branch and aligned with underleaves of branch. Ventral-intercalary branching not seen. Leaves rigid, brittle, concave, imbricate and completely obscuring stem in dorsal view or nearly so, 0.9–1.2 mm long at longest point, 1–1.6 mm wide at widest point, spreading, the insertion weakly to moderately incubous, recurved at dorsal end; ventral lobe often aligned with lateral underleaf lobes, ± decurrent on the stem or the lobe with a decurrent lobuliform flap. Leaves distinctly asymmetric, unequally 4(5)-lobed and variously appendaged, the leaves divided to ca. 0.5–0.85 (median sinus), the distance from dorsal sinus base to insertion much greater than that from the median and ventral sinuses to insertion. Lobes narrowly acute to attenuate to acuminate, the dorsal pair of lobes paired, the 2 ventral widely divergent from the united dorsal lobes (when flattened), the ventral 1 or 2 lobes often ventrally sulcate, subfalcate, sometimes with a tooth, the lobes terminating in several laterally juxtaposed cells, or a single cell or a uniseriate row of 2–3 cells, the cells of uniseriate row ± isodiametric, thick-walled; dorsal lobes entire, usually narrowing to a sharp apex, 8–14 cells wide at base; ventral and median sinuses reflexed, with accessory armature often present in the sinus base. Disc distinctly asymmetric, 20–25(31) cells high at dorsal sinus, 8–10 cells high at ventral sinus, the dorsal margin broadly ampliate, often distinctly auriculate at the base, sporadically with a tooth or spine near the base, the ventral margin subcordate to subauriculate, typically with accessory armature. Accessory lamellae sometimes present on the abaxial face of disc, descending from sinus bases. Flattened paraphyllia-like, irregularly dentate appendages often present on base of disc. Cells of disc-middle with moderately thickened walls, with intermediate thickenings and medium and straight-sided to large and bulging trigones, 19–27 μm wide × 28–40 μm long; median basal cells larger, in a single, sometimes indistinct row; surface smooth to finely striate-papillose. Oil-bodies occupying small portion of cell lumen, hyaline and glistening, (2)3–4 per median and upper disc cells, distinctly botryoidal, irregularly ellipsoid to oblong to fusiform to slightly crescentic, 3.5 × 8 μm to 5–6 × 12–15 μm or, in equal numbers spherical and 3.5–5.5 μm in diam., the basal cells with 4 oil-bodies per cell, more coarsely botryoidal, with as few as 3–7 spherules, 5.5–7 × 13–14 μm. Underleaves plicate, widely spreading, symmetrically 4-fid to ca. 0.5–0.6 (median sinus), the lobes typically ventrally sulcate, with strongly reflexed sinus bases, accessory lamellae, and flattened paraphyllia similar to those of the leaves; lobes short-attenuate, the margins entire to irregularly crenulate, often bluntly rounded at the tip or terminating in a uniseriate row of 2(3) cells; disc 8–10 cells high at median sinus, the margins reflexed, subauriculate at base, decurrent, often toothed.

Plants dioecious. Androecia determinate, on tightly spicate, often cernuous ventral-intercalary branches from main shoot and primary branches (in leafy sectors); bracts ventricose-cucullate,

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Lepidozia setigera Steph. Upper disc cell. 4. *Lepidozia obtusiloba* var. *parvula* J.J.Engel. Cells of disc. 5. *Lepidozia ornata* J.J.Engel. Basal cell of lobe. 6. *Lepidozia laevifolia* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees. Basal cell of lobe. (Fig. 1, from *Glenny 9148*, New Zealand, South Is., Westland EP, Big Wainihinihi R.; 2, from *Glenny 9084*, New Zealand, South Is., Canterbury EP, Mt. Aicken; 3, from *Glenny 9415*, New Zealand, South Is., Western Nelson EP, Brunner Ra.; 4, from *Glenny 9134*, New Zealand, South Is., Westland EP, Mt. Turiwhate, near summit; 5, from *Glenny 9138a*, New Zealand, South Is., Westland EP, Mt. Turiwhate; 6, from *Glenny 9088*, New Zealand, South Is., Canterbury EP, Mt. Aicken.)

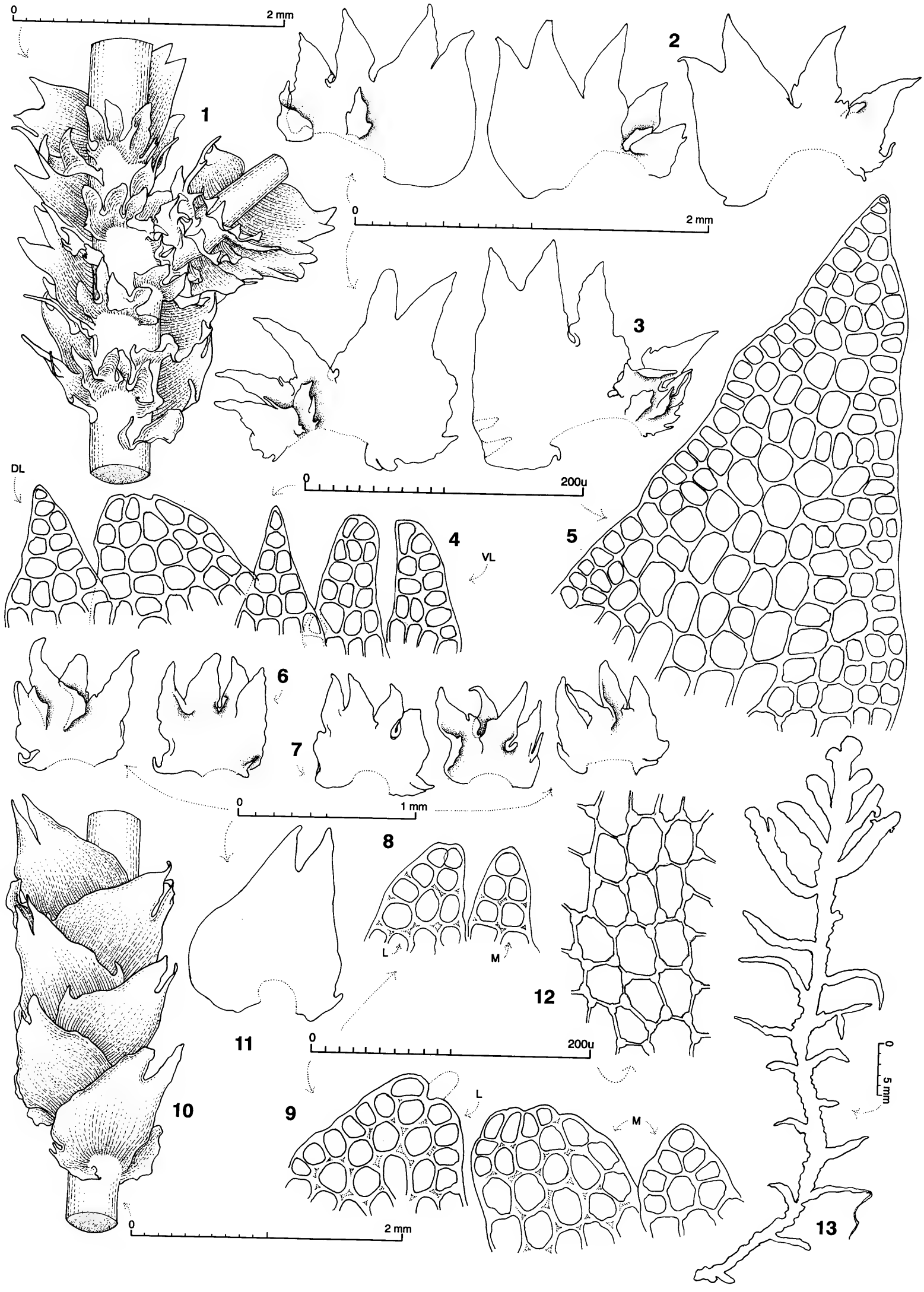

Fig. 35.
Lepidozia ornata J.J.Engel. 1. Sector of main shoot with *Frullania*-type branch, ventral view. 2, 3. Leaves. 4. Apical sectors of 5 lobes from same leaf (DL = dorsal lobe; VL = ventral lobe). 5. Second dorsal-most leaf lobe. 6, 7. Underleaves. 8. Apical sectors of lateral (= L) and median (= M)

2-lobed to ca. 0.3, the lobes broad acute, at times apiculate; antheridial stalk biseriate. Gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (530 m), South Island (610–1525 m), North Island (1200 m). Known from Fiordland, Otago (Blue Mtns.), Westland, Canterbury (Hooker Valley) and Volcanic Plateau (Mt. Ruapehu) EPs.

This species is nearly always penalpine–alpine and occurs under snow tussock (*Chionochloa*) cover (often on damp ground between tussock bases), particularly on damp slopes or stream banks (perhaps requiring adequate drainage). Also present over leaf litter at the edges of tarns, in crevices of cliff faces, and in pockets of banks. The sole record of the species in South Island forests is from the upper reaches of an open *Nothofagus menziesii* forest at 610 m at Moraine Creek, where it forms thick deep masses on the sides of bryophyte mounds. On Stewart Island the species was found in a deep, protected niche at 530 m at the summit of Mt. Rocky, an area of very exposed, prominent rocky outcrops, with wind-pruned heath dominated by *Leptospermum scoparium* up to ca. 50 cm high.

Comments: The combination of brown plants with ornamented leaves and underleaves will immediately distinguish this plant. Leaves and underleaves are variously appendaged with accessory lobes, paraphyllia-like appendages and lamellae (Fig. 35: 1–3, 6, 7, 10). The decurrent ventral extremity of the leaf often extends to the ventral stem midline, and at times is ornamented with accessory lobes (Fig. 35: 1). The ventral and median sinus bases of leaves and sinus bases of underleaves are frequently broadly dilated and the reflexed margins of the lobes often extend downward as irregular lamellae on the abaxial face of the disc. The flattened paraphyllia-like appendages often at the base of the disc are present in no other New Zealand species of *Lepidozia*.

See also comments under *Lepidozia obtusiloba*.

Lepidozia concinna Colenso

[Fig. 36]

Lepidozia concinna Colenso, Trans. & Proc. New Zealand Inst. 18: 244. 1886. Type: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1417* (BM!, WELT!).
Lepidozia latiloba Colenso, Trans. & Proc. New Zealand Inst. 19: 287. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso a. 1421* (BM!, WELT!).
Lepidozia colensoana Steph., Sp. Hepat. 3: 597. 1909, *syn. fide* Engel and Schuster (2001). Type: New Zealand, Lake Waikare, *Colenso 1021* (G! – *c. per.* + *seta*).

Plants procumbent, the stems interwoven, rather flexuous, with spreading branches, green, highly nitid, the shoots medium, to 1.7 cm wide, including branches. Branching nearly exclusively of *Frullania* type, often long, closely and regularly pinnate, the primary branches often becoming whip-like, flagelliform, microphyllous and rooting in the substrate, with secondary branches occasional; branch half-leaf symmetrical, cordate, 2-lobed to ca. 0.3; first branch

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lobes of same underleaf. 9. Apical sectors of median (= M) and lateral (= L) lobes of same underleaf. 10. Sector of main shoot, dorsal view. 11. Half-leaf. 12. Median disc cells of leaf. 13. Outline of shoot at low magnification. (Figs. 1, 3–7, 10, 12–13, from type; 2, 8–9, 11, from *Engel 18799*, New Zealand, South Is., Fiordland EP, Mistake Creek.)

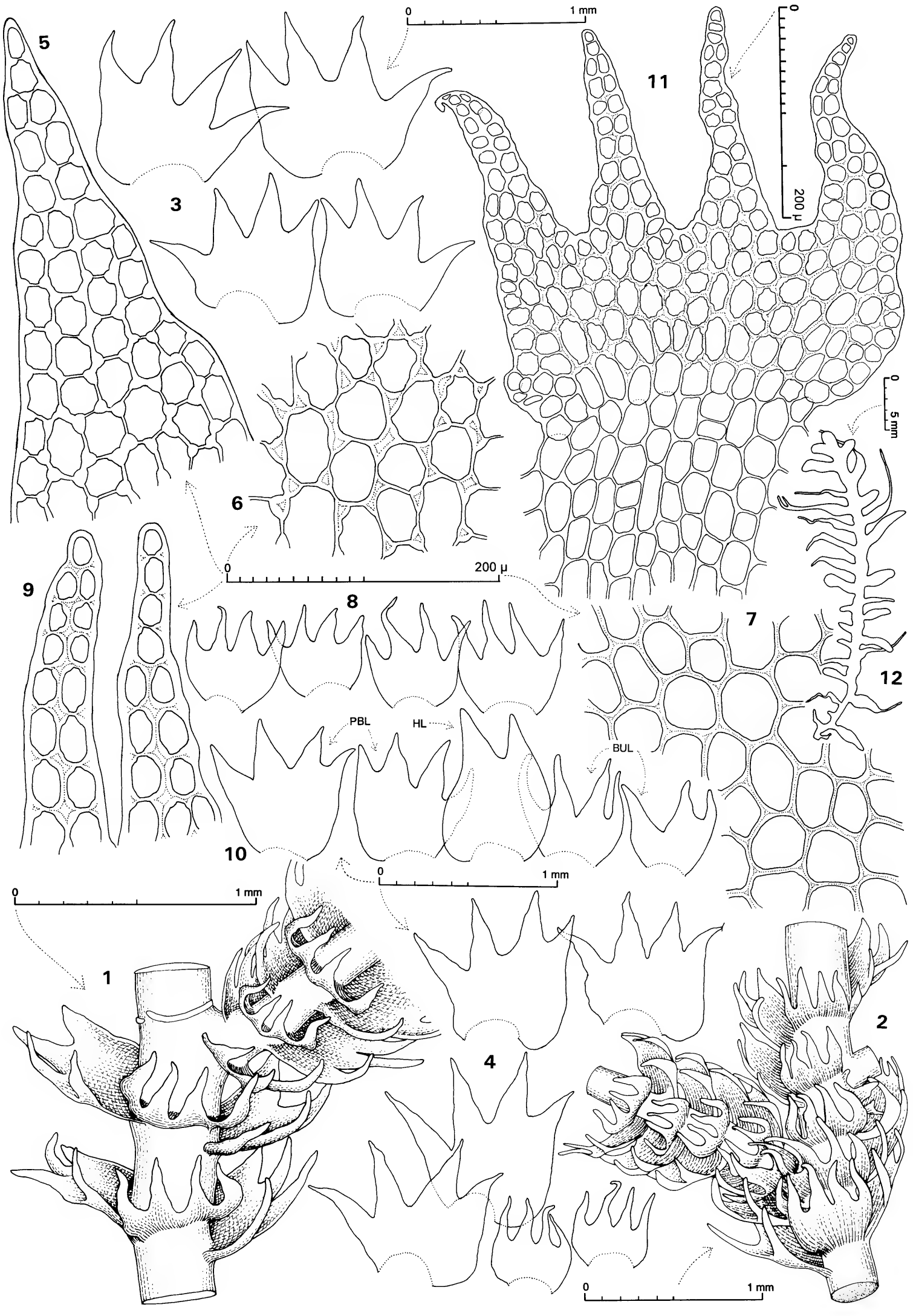

Fig. 36.
Lepidozia concinna Colenso. 1. Portion of main shoot with *Frullania*-type branch, ventral view; note position of first branch underleaf. 2. Portion of main shoot with 2 *Frullania*-type branches, ventral view. 3. Leaves. 4. Four leaves and (lower right) 2 underleaves at same scale. 5. Dorsal lobe

underleaf 2–4-lobed, inserted on ventral to ventral-lateral side of branch and aligned with underleaves of branch. Ventral-intercalary branching occasional, leafy. Leaves when dry curved ventrally, the shoots (particularly branches) then appearing braided, the main shoot leaves concave, loosely imbricate and not obscuring stem in dorsal view, 0.6–0.85 mm long at longest point, (0.7)0.8–1 mm wide at widest point, spreading, the insertion weakly to strongly incubous; leaves variable in shape on the same stem, subsymmetrical to weakly asymmetrical (except for the ampliate dorsal base), subequally 4(5)-lobed, the leaves divided to ca. 0.4–0.6 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the dorsal sinus shallow or the sinuses gradually becoming deeper ventrally. Lobes acute to apiculate, entire, terminating in a uniseriate row of 2–3(6) cells, the cells of uniseriate row ± isodiametric, thick-walled; dorsal lobes 5–7(9) cells wide at base; surface of lobes smooth or finely striate-papillose. Disc subsymmetric, 12–19 cells high at dorsal sinus, 9–11 cells high at ventral sinus, the margins entire, the dorsal margin ampliate but not strongly so, ± cordate at the base, the ventral not much shorter than the dorsal. Cells in a well-defined, large median field, ± isodiametric to occasionally oblong-hexagonal, thick-walled, trigones medium and straight-sided to large and bulging (rarely weak and concave-sided), (24)26–41 μm wide × (32)34–45(49) μm long; cells of the ampliate portion smaller; median basal cells not sharply differentiated; surface of disc smooth. Oil-bodies (Engel and Schuster, 2001) in median/subapical cells (1)2–5(6) per cell, coarsely botryoidal, small, spherical to ovoid, 3.6–4 × 3.6–5 μm up to 5 × 11 μm; basal cells with 4–8 oil-bodies of similar size (4 × 5 μm to 4.5–5 × 6–9 μm). Underleaves inserted on 10 rows of stem cells, widely spreading, ca. 1–1.2× stem width, narrowed to insertion, symmetrically 4-fid to ca. 0.45–0.55 (median sinus), the lobes incurved, plane, somewhat spreading, slenderly attenuate, entire, terminating in a single cell or uniseriate row of 2–3(5) cells; disc 7–9 cells high at median sinus, the margins plane, broadly curved, entire. Fungal partner an ascomycete.

Androecia not seen. Perianth (*fide* Stephani, 1898–1924 [1909]) broadly oblong, the mouth constricted and entire; capsule broadly oval; spores 18 μm in diam., reddish brown; elaters bispiral, laxly twisted.

Distribution and Ecology: New Zealand: South Island (150–915 m), North Island (650–920 m); Australia: Tasmania. In New Zealand known from Fiordland, Otago, Westland, Sounds–Nelson (Richmond Ra.), Volcanic Plateau (Tongariro Natl. Park, Waiotapu) and Gisborne (Urewera Natl. Park) EPs.

A forest plant, often in extensive patches and becoming abundant, occurring on old, decaying logs or, less often, over soil; the species occurs along a broad elevational gradient (150–920 m).

Comments: The leaves of *Lepidozia concinna* typically are subsymmetrically to weakly asymmetrically lobed, with the lobes not notably—and never consistently—in pairs (Fig. 36: 3, 4). The underleaves are somewhat wider than the stem, narrowed to the insertion (Fig. 36:

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of leaf. 6, 7. Median disc cells of leaf. 8. Underleaves (drawn at same scale as fig. 4). 9. Apical sectors of 2 median lobes of same underleaf. 10. Primary branch leaves (= PBL), half-leaf (= HL) and first branch underleaves (= BUL). 11. Portion of stem with underleaf; note ventral merophyte width of 10 cells. 12. Outline of plant at low magnification. (Figs. 1, 4, 7, 11, from *Engel 23201*, New Zealand, South Is., Fiordland EP, immediately N of Ten Mile Bush, near W shore of Lake Te Anau; remainder from *Child 4373*, New Zealand, South Is., Sounds–Nelson EP, Red Hills.)

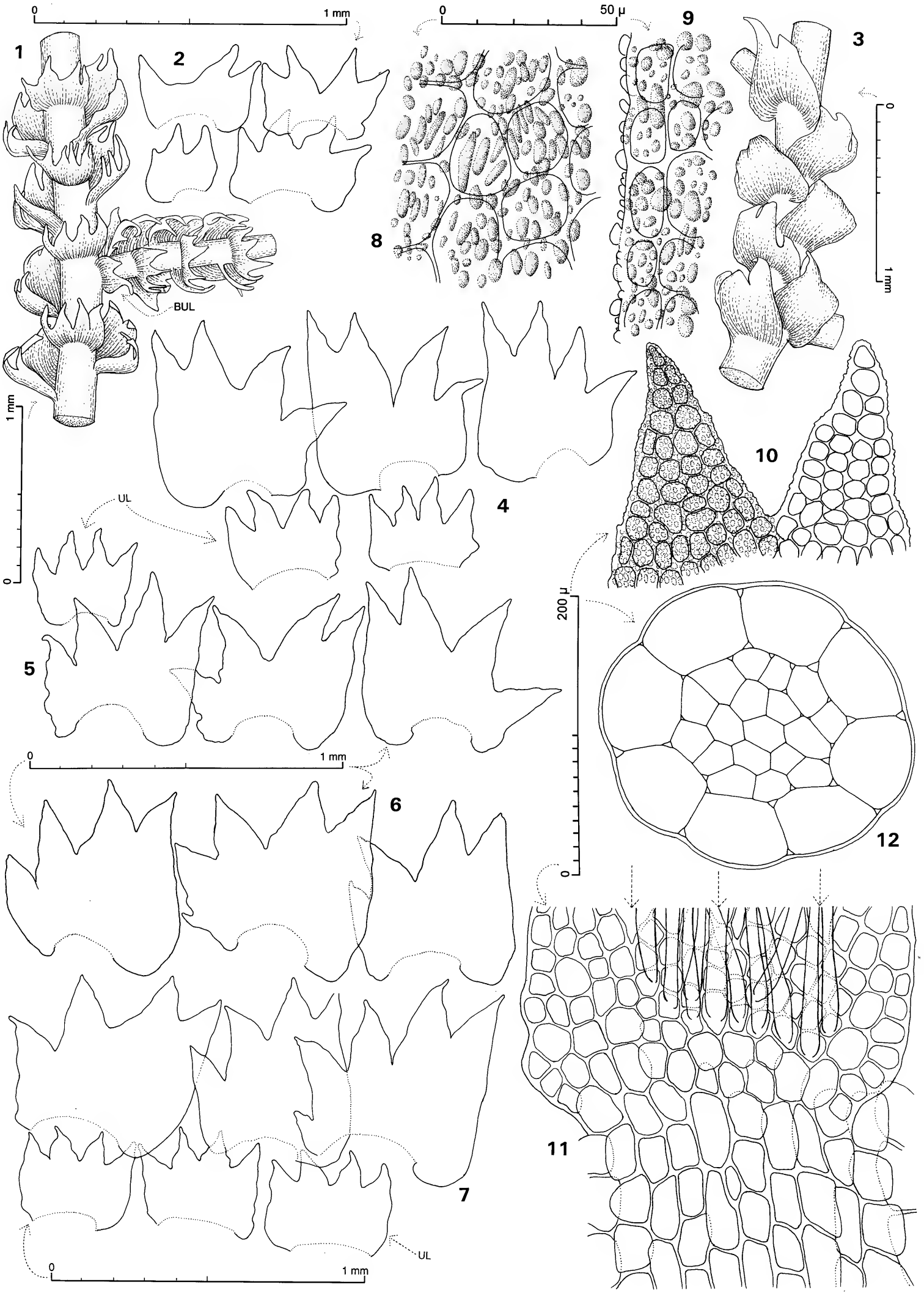

Fig. 37.
Lepidozia laevifolia (Hook.f. & Taylor) Gottsche, Lindenb. & Nees (figs. 6, 7, from var. *acutiloba*; remainder from var. *laevifolia*). 1. Sector of main shoot with *Frullania*-type branch, ventral view (BUL = first branch underleaf). 2. First branch underleaves. 3. Sector of shoot, dorsal view. 4–7. Leaves and underleaves (= UL), all drawn at same scale. 8. Median disc cells showing surface

1, 2), inserted on 10 rows of stem cells (Fig. 36: 11), and with the lobes slenderly attenuate and often broadly incurved (Fig. 36: 1, 2). A notable feature of this species is the well-defined median field of large disc cells (to 40 μm wide); the cells are in large part ± isodiametric and typically have medium to large and bulging trigones (Fig. 36: 6, 7). *Lepidozia concinna* is usually readily recognized because of the deeply lobed underleaves, with attenuated lobes, often 3–4 cells broad at the base (Fig. 36: 8, 11). The plants are uniformly green, lacking secondary pigmentation, which will immediately distinguish this species from the *L. obtusiloba* complex.

Lepidozia laevifolia (Hook.f. & Taylor) Gottsche, Lindenb. & Nees

[Fig. 34: 6, oil-bodies, p. 220; Figs. 37, 38]

Jungermannia laevifolia Hook.f. & Taylor, London J. Bot. 3: 385. 1844 (3: 285. [*sic*] *in errore pro* 385). *Lepidozia laevifolia* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 208. 1845. *Mastigophora laevifolia* (Hook.f. & Taylor) Trevis., Cat. Herb. Crypt. Trevisan 2: 30. 1853. Lectotype (*fide* Engel and Schuster, 2001): Campbell Is., Nov. 1840, *Hooker* (FH!).

Lepidozia minuta Colenso, Trans. & Proc. New Zealand Inst. 18: 245. 1886, *non L. minuta* Steph., Sp. Hepat. 3: 603. 1909. Type: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1419* (BM!, G – *absens*, WELT!).

Lepidozia retrusa Colenso, Trans. & Proc. New Zealand Inst. 22: 455. 1890 (1889). Type: New Zealand, Waipawa Co., S of Dannevirke, 1889, *Colenso a. 1515* (BM! – *c. sporo.*, G – *absens*, WELT! – *c. per.*).

Lepidozia papillata Steph., Sp. Hepat. 3: 595. 1909. Type: Auckland Is., *Hooker* (G!, "sub *Lepid. dispar*").

Lepidozia asperifolia Steph., Sp. Hepat. 3: 596. 1909. Type: New Zealand, South Is. (*non vidi*).

Plants closely prostrate, flexuous, with spreading branches, green, nitid when dry, the shoots small, to 1 cm wide, including branches; exceptionally luxuriant phases to 2.5 cm long × 0.9 cm wide. Branching nearly exclusively of *Frullania* type, rather short, normally irregularly and distantly pinnate, ± regularly pinnate in well-developed plants, the primary (and secondary) branches sometimes becoming whip-like, flagelliform and microphyllous; secondary branches occasional; branch half-leaf subsymmetrical, cordate, 2-lobed to ca. 0.25; first branch underleaf (1)2–4-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, in both cases the first branch underleaf aligned with underleaves of branch. Ventral-intercalary branching occasional, leafy, at times becoming leading shoots. Stems flexuous, the cortical cells in 1 layer of thick-walled cells somewhat larger than the thick-walled medullary cells. Leaves when dry deeply cup-shaped, with the tips

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papillae. 9. Marginal cells of ampliate sector of disc. 10. Leaf lobes showing surface papillae in lobe at left. 11. Portion of stem with underleaf disc and lobe bases; note ventral merophyte width of 10 cells and rhizoid origin (arrows indicate sinus bases). 12. Seta, cross section. (Figs. 1–3, from *Engel 18406*, New Zealand, South Is., Arthur's Pass Natl. Park, Kelly Ra.; 4, 8–10, from type of *L. laevifolia*; 5, from *Engel 20585*, New Zealand, North Is., Gisborne EP, Urewera Natl. Park, Waikareiti Track; 6, from *Engel 22816*, South Is., Westland EP, road to Rainbow Skifield in vicinity of Red Gate, just W of Wairau R.; 7, from type of var. *acutiloba*; 11, from *Engel 22885*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Bealey Valley Track; 12, from *Child 2849*, New Zealand, South Is., Otago EP, Maungatua.)

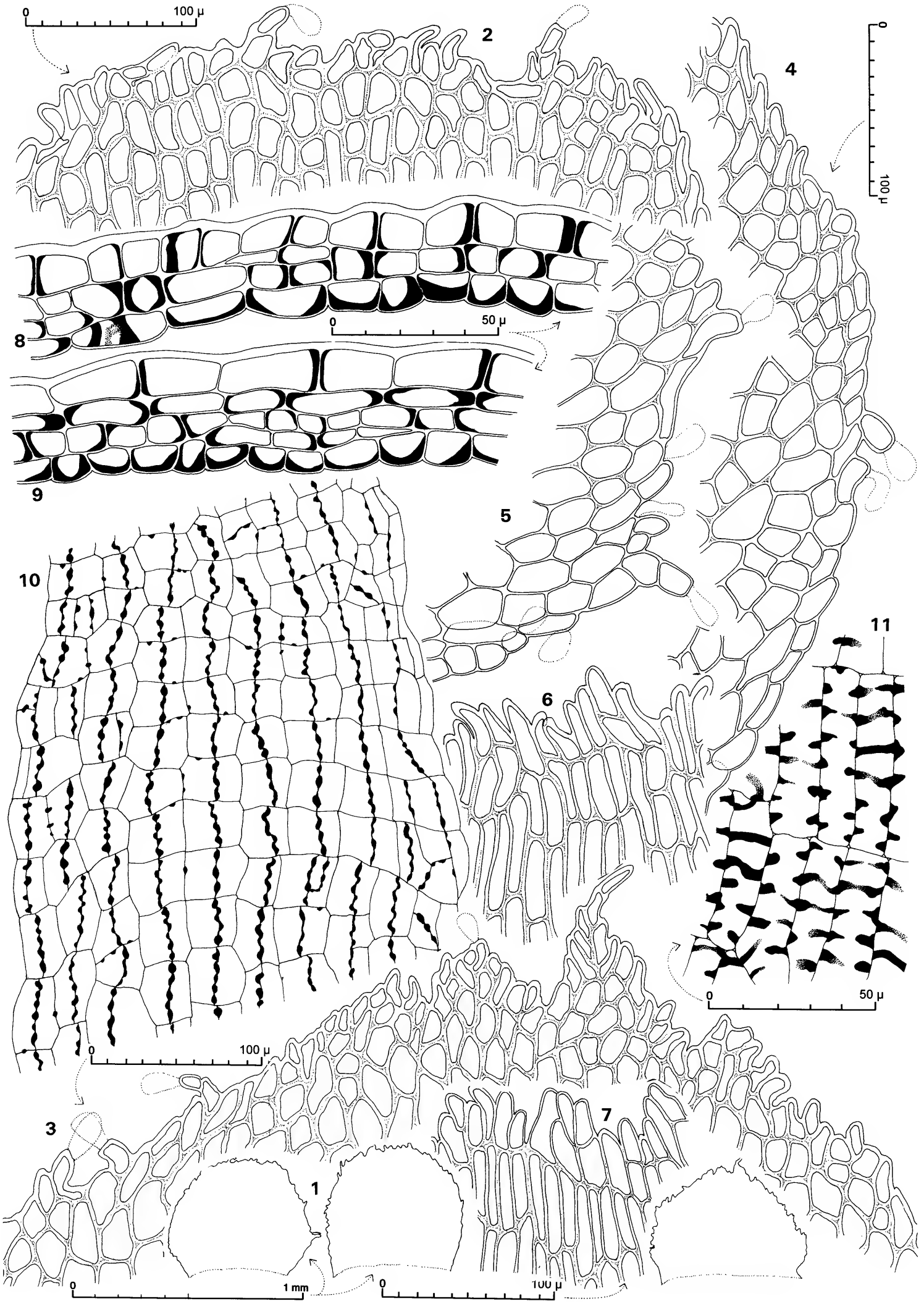

Fig. 38.
Lepidozia laevifolia (Hook.f. & Taylor) Gottsche, Lindenb. & Nees. 1. Two bracts and (to right) bracteole from innermost series (all drawn to same scale). 2, 3. Portions of apex of 2 innermost bracts. 4, 5. Complete lateral margin and basal half of margin, respectively, of innermost bracts (drawn to same scale). 6, 7. Portions of perianth mouth (drawn to same scale). 8, 9. Capsule, cross

of the lobes incurved and not visible in dorsal view; leaves when moist rigid, distinctly concave, contiguous, with much of stem visible in dorsal view, 0.5–0.65 mm long at longest point, 0.5–0.7 mm wide at widest point, spreading, the insertion distinctly incubous; leaves variable, subsymmetric to distinctly asymmetric, subequally 4(6)-lobed, sometimes with a ± shallow dorsal sinus, the leaves divided to ca. 0.4–0.65 (median sinus), the distance from dorsal sinus base to insertion ± equal to or much greater than that from ventral sinus to insertion. Lobes broadly to narrowly acute, sometimes short-apiculate, the lobe margins entire to somewhat sinuate to occasionally 1–2-dentate, terminating in a single cell or a uniseriate row of 2–3 non-elongated, thick-walled cells; dorsal lobe 5–10 cells wide at the base (at times 4 cells wide in minute phases). Disc subsymmetric to asymmetric and then obliquely truncate, 12–18 cells high at dorsal sinus, 4–9 cells high at ventral sinus; dorsal margin ampliate, cordate to auriculate at the insertion (rarely decurrent), entire to sinuate, sometimes irregularly crenulate to dentate; ventral margin shorter than the dorsal, ± cordate at the insertion, entire or sometimes with an accessory lobe. Cells evenly thick-walled, occasionally with small trigones, the cells of median portion of disc 16–25(28) μm wide × 19–32 μm long, ± longitudinally elongated, typically sharply differentiated from the small and isodiametric (8–10 μm) cells of the lobes and ampliate sector of the disc; marginal cells of disc and lobes lacking a thickened outer wall; surface coarsely and closely papillose on lobes and ampliate sector, the disc closely striate-papillose. Oil-bodies hyaline, 2–4(5) per cell at base of dorsal pair of lobes (and also midleaf), 2–4(5) at leaf base but larger there, botryoidal, irregularly ellipsoidal, 4–5 × 7 μm to 4–6 × 10–10.5 μm, or spherical and 4–5.5 μm in diam. Underleaves inserted on 6–8 rows of stem cells, spreading, short, broader than high, symmetrically 4-fid to ca. 0.3–0.45 (median sinus), the lobes plane, entire, acute to acuminate, terminating in a single cell or a uniseriate row of 2–4 cells; disc 7–8 cells high at median sinus, cordate at the insertion, the margins plane, entire. Fungal partner an ascomycete.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, sometimes cernuous ventral-intercalary branches from main shoot or terminal on long-flagelliform primary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.4, the lobes acute to apiculate; antheridial stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, suborbicular to broadly ovate to suboblate; apices with 4 small teeth hardly differentiated from the otherwise crenate-denticulate apex or with (2)4 short, rather irregular lobes, the lobes finely and sparingly crenulate; lamina margin bordered by cells of variable shape, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate to the base; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth; mouth cells rather thick-walled, at the apical end laterally free for varying lengths, the mouth thus crenate-denticulate.

Seta with 8 rows of outer cells surrounding an inner core of 18 much smaller cells. Capsule wall 30–35 μm thick, of 3–4 or 4–5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings alternating with those that are

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sections of 3–4- and 4–5-stratose walls. 10. Capsule wall, outer layer (× 204). 11. Capsule wall, inner layer. (All from *Engel 20669*, New Zealand, North Is., Gisborne EP, Urewera Natl. Park, crest trail from Highway 38 toward Whakataka summit.)

devoid of thickenings (or are rarely locally thickened), the transverse walls usually devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, with nodule-like to spine-like thickenings common, with semiannular bands weakly developed, only occasionally present, often incomplete, pale.

Spores 11.5–13.4 μm in diam., spore wall light brown, with dense, rather coarse, sharply defined, rather broad papillae and simple or furcate vermiculate markings. Elaters ± rigid to feebly tortuous, 9.6–10.1 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.4–3.8 μm wide.

Comments: Small, poorly developed plants of *Lepidozia laevifolia* and *L. pumila* may be difficult to distinguish satisfactorily. Both species can have distinctly concave leaves with the lobes incurved and hidden when viewed in dorsal aspect. Well-developed leaves should always be selected for examination, but a number of leaves should also be examined to determine the range of variation. The leaves of *L. laevifolia* are nearly always coarsely papillose (Fig. 37: 8–10). Distinctly papillose leaves may vary in the number of papillae per cell: some populations have very coarse papillae that number ca. 7–8 or 12–15 per cell (Fig. 37: 8). Other populations are less coarsely papillose, with ca. 30 papillae per cell. The dorsal leaf margin in *L. laevifolia* is usually ampliate and distinctly cordate at the insertion, the margins of the disc and lobes are sinuate, and the cells of the ampliate portion are small and abruptly differentiated from the cells of the disc. Typically, in *L. pumila* the surface is smooth, and the dorsal leaf margin is straight and abruptly cordate at the base (Fig. 42: 1, 4, 5); the leaf cells appear large in proportion to the size of the leaf, giving the leaf a "cellular" appearance. Another useful character in distinguishing *L. pumila* from *L. laevifolia* is the presence in the former species of a thickened outer wall of at least some of the marginal cells of disc and lobes (Fig. 42: 6, 8).

The species is separable into three varieties, as follows:

Key to the varieties of *L. laevifolia*

1a. Dorsal half of leaf more deeply bilobed (typically to 0.2 or more); disc cells moderately and evenly thick-walled, occasionally with small trigones 2
  2a. Leaf lobes narrowly acute, the two dorsal lobes separated by a narrow, rather deep sinus (less than 45°); median disc cells large, 18–25(28) μm wide; leaf margins sinuate to occasionally 1–2-dentate; underleaf lobes slenderly acuminate; leaves ± strongly asymmetrical. Occurring at (60)300 m to penalpine zone . . . . . var. *laevifolia* (p. 231)
  2b. Leaf lobes broadly acute, the two dorsal lobes separated by a broad, shallow sinus (45–90°); median disc cells narrow, 16–20 μm wide; leaf margins often sinuate, never toothed; underleaf lobes acute to broadly acuminate; leaves weakly asymmetric. Occurring in upper montane forests to alpine zone . . . . . .var. *acutiloba* (p. 231)
1b. Dorsal half of leaf very shallowly bilobed (to 0.15–0.2); disc cells evenly and very strongly thick-walled, trigones absent . . . . . var. *alpina* (p. 232)

Lepidozia laevifolia var. ***laevifolia***

Leaves ± strongly asymmetrical, obliquely truncate, 4(6)-lobed, divided to 0.5–0.65 (median sinus); leaf lobes narrowly acute, the two dorsal lobes ± paired, separated by a narrow, rather deep sinus (less than 45°); disc 12–15 cells high at dorsal sinus, 4–7 cells high at ventral sinus, the ventral sinus often ± reflexed; leaf margins occasionally 1–2-dentate; median disc cells 18–25(28) μm wide; underleaf lobes slenderly acuminate, at times only 2–3 cells wide at base.

Distribution and Ecology: Amphi-Pacific-temperate. Macquarie Island; New Zealand: Campbell Island, Auckland Islands, Stewart Island (70–530 m), South Island (300–1370 m), North Island (60–1390 m), Chatham Islands; Australia: Tasmania, Victoria, New South Wales; Kerguelen Island, Marion and Prince Edward Islands, Falkland Islands, southern South America, Juan Fernandez Islands. In New Zealand known from Fiordland, Otago, Westland, Canterbury, Sounds–Nelson, Volcanic Plateau, Gisborne, Auckland and Northland EPs.

In New Zealand var. *laevifolia* typically ranges from middle-elevation forests to the penalpine zone, and is able to tolerate considerable exposure. However, it may be present in lower-elevation forests, and extends as far north as Radar Bush (WSW of Cape Reinga, 100 m), where it occurs on rotted, decorticated logs in forests of *Beilschmiedia – Vitex – Hoheria* and *Cyathea dealbata*. Also present in the Kiwanis Reserve (S of Kaitaia, ca. 60–80 m) on *Rhopalostylis sapida* in mixed broadleaf forest dominated by *Beilschmiedia* and *Vitex*, with *Rhopalostylis*, *Coprosma*, *Dacrycarpus dacrydioides* and *Hoheria*. The variety, however, is less common below 300 m. In forests it occurs on shaded, moist cliff faces and boulders, soil banks (including banks of roadcuts through the forest, and here at times mixed with *Breutelia elongata*), rotted logs, and, occasionally, over bark. It is rather common on the floor and loosely on bark at the bases of *Leptospermum scoparium* in the Otupaka Stream frost flats southwest of Minginui. In penalpine situations it occurs on soil under and in between tussocks (at times where the tussock base is rotted), under shrub cover, in boulder fields, on cliff faces (where sometimes forming sheets) and on clayey banks. In boggy sites it may occur among *Sphagnum*, and then the shoots are often quite straggly.

Lepidozia laevifolia var. ***acutiloba*** J.J.Engel

Lepidozia laevifolia var. *acutiloba* J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 61. *f. 20: 6, 7*. 2001. Holotype: New Zealand, South Is., Otago Prov., W slope of Flagstaff, NW of Dunedin, 560 m, *Engel 17632* (F); isotype: (CHR).

Leaves weakly asymmetrical, ± equally 4(6)-lobed, divided to 0.35–0.5 (median sinus); leaf lobes broadly acute, the two dorsal lobes separated by a broad, often shallow sinus (45–90°), the disc 16–19 cells high at dorsal sinus, 6–10 cells high at ventral sinus; leaf margins often sinuate but rarely toothed; median disc cells small, 16–20 μm wide; underleaves shallowly lobed, the lobes acute to broadly acuminate.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5 m), South Island (560–1450 m), North Island (650–1300 m). Known from Fiordland, Southland, Otago, Westland, Canterbury, Volcanic Plateau and Gisborne EPs.

Typically an upper-elevation plant, occurring in *Nothofagus menziesii* scrub at treeline and extending into the penalpine and alpine zones. It occurs on damp ground, sometimes appear-

ing as a pioneer, at other times between tussocks or over leaf litter under shrubs; also on damp cliff faces, rock outcrops and in rock crevices, etc. In the forest zone it may be terricolous or corticolous, as well as occurring on rotted logs, particularly where there has been soil accumulation. The variety occurs near sea level on Stewart Island over sandy soil in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall, and dense communities of *Gleichenia dicarpa* and *Empodisma minus* (track to Mason Bay, 1–1.8 km W of Freshwater Landing).

Lepidozia laevifolia var. ***alpina*** R.M.Schust. & J.J.Engel

Lepidozia laevifolia var. *alpina* R.M.Schust. & J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 62. *f. 22*. 2001. Holotype: New Zealand, South Is., Fiordland Natl. Park, Gertrude Cirque NE of Homer Tunnel, below saddle on W-facing exposed cliff, 1945 m, *Schuster 95-2089* (herb. Schuster).

Plants 500–550 to 760–810 μm wide with leaves, rather remotely pinnate, the branches in small part becoming flagelliform, rhizoidous; leaves strongly asymmetrically bifid, with each lobe again bifid, ca. 380–420 μm wide × 440–480(500) μm long; dorsal half of leaf much larger and longer than ventral half, ca. 0.15–0.2(0.25) bilobed, the lobes acute but not strongly so, ending in 2–3 subisodiametric or isodiametric cells; cells of disc strongly and evenly thick-walled, trigones lacking, the median disc cells (18)20–26 μm wide; surface papillose (at times obscurely so).

Distribution and Ecology: Endemic to New Zealand. Known only from type plants, which occurred admixed with *Herbertus oldfieldianus* and *Gymnomitrion strictum*, creeping amidst *Hymenophyllum*.

Comments: The var. *alpina* is similar to var. *acutiloba*, also of higher elevations, in the shallow dorsal-most sinus and the broadly acute lobes. The var. *alpina* differs from var. *acutiloba* in the exceptionally shallow dorsal-most sinus, in the exceedingly thick-walled leaf cells, and in the somewhat larger median disc cells ([18]20–26 μm wide vs. 16–20 μm wide in var. *acutiloba*). Also, in var. *alpina* the dorsal-most sinus tends to be narrower than in var. *acutiloba* and may even be slit-like.

Variety *alpina* has distinctly thick-walled cells reminiscent of *Lepidozia pumila*. However, the var. *alpina* has shorter and much less tapered dorsal leaf lobes, separated by a rather shallow sinus. Also, unlike *L. pumila*, the sinus separating the two dorsal lobes is usually much shallower than that separating the two ventral lobes. In *L. pumila* the dorsal sinus descends ca. 0.3–0.35 the leaf length, in var. *alpina* only about (0.15)0.2–0.25 the leaf length. Moreover, *L. pumila* lacks an auriculate dorsal leaf base, has larger disc cells (to 33 μm wide vs. at most 26 μm wide in var. *alpina* and has ventral merophytes 5–6 cells wide vs. 6–8 cells wide in var. *alpina*.

Lepidozia fugax J.J.Engel

[Fig. 39]

Lepidozia fugax J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 63. *f. 23*. 2001. Holotype: New Zealand, South Is., Otago/Westland Prov. boundary, Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel 18023* (F); isotype: (CHR).

Plants loosely prostrate, in pure mats, rather stiff and wiry, with spreading branches, green, distinctly nitid when dry, the shoots small, to 1.2 cm wide, including branches (shoots with rigorous branches), shoots with short branches at times only 3 mm wide. Branching nearly exclusively of *Frullania* type, short to rather long, irregularly 1(2)-pinnate, the primary (and secondary) branches sporadically to frequently becoming whip-like, flagelliform and microphyllous; secondary branches occasional; branch half-leaf subsymmetrical, the basal sector somewhat rounded to subcordate, 2-lobed to ca. 0.3; first branch underleaf 2–3-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, in both cases the first branch underleaf ± aligned with underleaves of branch. Ventral-intercalary branching occasional, leafy. Leaves fragile and easily detached, moderately concave when dry, the dorsal lobes stiffly spreading, the tips of the ventral lobes usually incurved and not visible in dorsal view; leaves when moist often with a ragged appearance, slightly concave, contiguous to imbricate, with much of stem visible in dorsal view, 0.3–0.5 mm wide and long, distinctly spreading, the dorsal margin forming an angle with stem as much as ca. 90°, the insertion distinctly incubous; leaves variable in shape, subsymmetric to moderately asymmetric, subequally to unequally 4(5)-lobed, the leaves divided to ca. 0.3–0.5 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion. Lobes acuminate, often appearing short in proportion to disc, the tips often caducous (lobes often lacking the uniseriate sector), the lobes often becoming slender and 2 cells wide for much of their length, the dorsal lobes 2–4 cells wide at the base; lobes entire, terminating in a uniseriate row of 2–4(5) at most somewhat elongated (to ca. 1.3:1) cells, the cells of uniseriate row turgid, barrel-shaped, the septa constricted, the terminal cell rounded at the tip; surface of lobes papillose. Disc moderately to distinctly asymmetric (the disc then obliquely truncate), 9–13 cells high at dorsal sinus, 6–7 cells high at ventral sinus; dorsal margin moderately ampliate, cordate at the insertion, mostly entire to sinuate, sporadically with a 1–2-celled blunt or sharp tooth; ventral margin subcordate at the insertion, entire or sometimes with a single tooth. Cells of median portion of disc with walls uniformly rather strongly thickened, trigones lacking, the cells 17–24 μm wide × 20–31 μm long, ± longitudinally elongated; cells of ampliate sector ± isodiametric; marginal cells of disc and lobes in surface view with a strongly thickened free wall (the wall often crescentic and bulging into the cell lumen), the disc cells in cross section with crescentic thickenings of the abaxial wall; disc cells in cross section with crescentic thickenings of the abaxial wall; surface of disc smooth. Underleaves inserted on 7 rows of stem cells, strongly spreading, ca. 1.5–2× stem width, broader than high, symmetrically 4-fid to ca. 0.3–0.5 (median sinus), the lobes slender, acuminate, the tips often caducous, terminating in a single cell or a uniseriate row of 2–3 cells; disc 5–7 cells high at median sinus, the margins plane, entire. Asexual reproduction by caducous tips of leaf lobes.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches from main shoot or submicrophyllous primary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes acute to apiculate, the lobe tips complete; antheridial stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, suborbicular to suboblate; apices with 4 small, rather irregular lobes, the lobes often finely and sparingly crenulate, the lobes often terminating in a uniseriate row of 2 narrowly rectangular cells or 2 laterally juxtaposed cells; lamina margin bordered by cells of variable shape, the apical or free end of marginal cells at times divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate in distal sector, the basal sector of bract margin entire except for slime papillae; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly

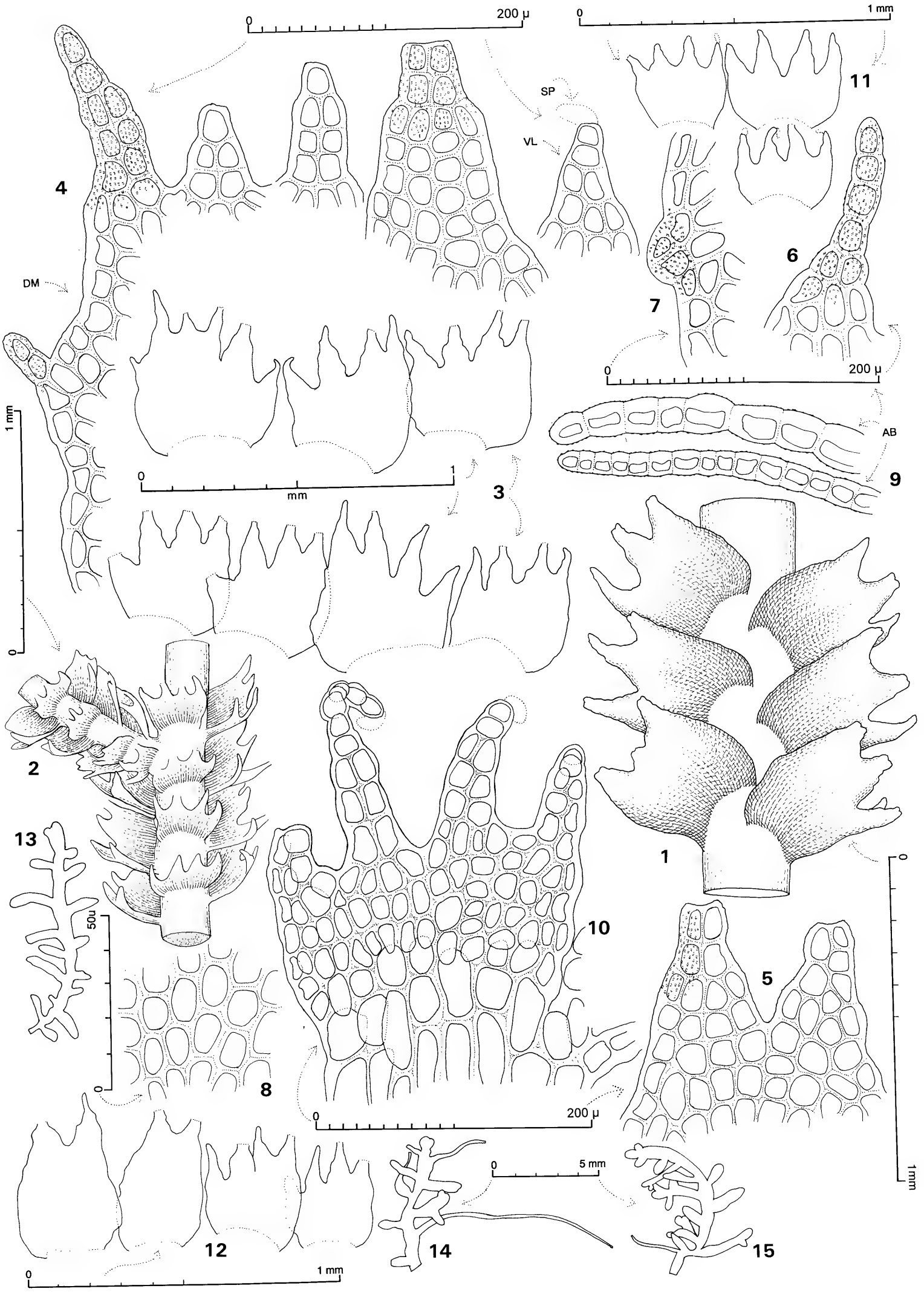

Fig. 39.
Lepidozia fugax J.J.Engel. 1. Sector of main shoot, dorsal view. 2. Sector of main shoot and *Frullania*-type branch, ventral view. 3. Leaves (note missing lobe tips). 4. Dorsal margin of leaf (= DM) and (left to right, i.e., dorsal to ventral) all lobes of same leaf (VL = ventral lobe; SP = slime

curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth; mouth cells rather thick-walled, papillose, at the apical end laterally free for varying lengths, the mouth thus crenate-denticulate.

Seta with 8 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule oblong, the wall 26–30 μm thick, of 3 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and several large nodules alternating with those that are devoid of thickenings (or are sporadically locally thickened), the transverse walls usually devoid of thickenings or sporadically have a sheet-like thickening or an isolated nodule; innermost layer of cells narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete.

Spores 12.4–13 μm in diam., the wall brown, with coarse, sharply defined, close papillae and short-vermiculate markings. Elaters rigid, nontortuous, 8.6–9.1 μm wide, only slightly and gradually tapering toward tips, bispiral to tips, the spirals 3.4–3.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (570–900 m). Known only from two collections; the type occurred on an erect, decorticated, rotted, 10-m-high tree remnant in a *Nothofagus menziesii* forest at 570 m (Haast Pass). A second collection was made in the upper limits of a *N. menziesii* forest, where it occurred mixed with *Telaranea* cf. *tetrapila* var. *roseana* on rotted wood at the base of a huge tree (Mt. Brewster, Mt. Aspiring Natl. Park, 900 m). Also known from the south branch of Big Gully, Ramy River, St. Arnaud, Nelson Lakes Natl. Park at 630 m. The fragmentary shoots occurred with *Dicranoloma billardierei* on very rotten wood/humus in mature *N. fusca – N. menziesii* forest with little understory but almost continuous ground tier of *Blechnum discolor* (*leg. T. Hay*, 29 Oct. 2004, AK).

Comments: The species is the only regional member of subg. *Notholepidozia* with caducous leaf tips (Fig. 39: 1, 3, 5), which give the plants a distinctive ragged appearance. The turgid, barrel-shaped cells of the uniseriate row and the constricted septa are responsible for the fragility of the lobes. The cells of the broken tips often have walls that have become secondarily thick-walled, rounded and papillose, following the breakage of the lobe tips.

As in *Lepidozia novae-zelandiae*, the abaxial cell walls of the disc and lobes are strongly thickened. These thickenings may also be viewed in a ventral aspect of the intact shoot, by focusing on the ventral margins of the lobes. In surface view, only the outer wall of the marginal cells of disc and lobes appears thickened (Fig. 39: 4).

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papilla; surface papillae shown in part). 5. Dorsal pair of lobes, the uniseriate sectors of each lobe having fallen away (surface papillae shown in part). 6. Second dorsal lobe (complete; note constricted septa). 7. Sector of dorsal margin of disc with a blunt tooth (surface papillae shown in part). 8. Median disc cells of leaf. 9. Leaf disc cross section (AB = abaxial face). 10. Portion of stem with underleaf; note ventral merophyte width of 7 cells. 11. Underleaves. 12. Two half leaves and (to right) 2 first branch underleaves. 13–15. Outlines of 3 shoots at low magnification (all at same scale). (All from holotype.)

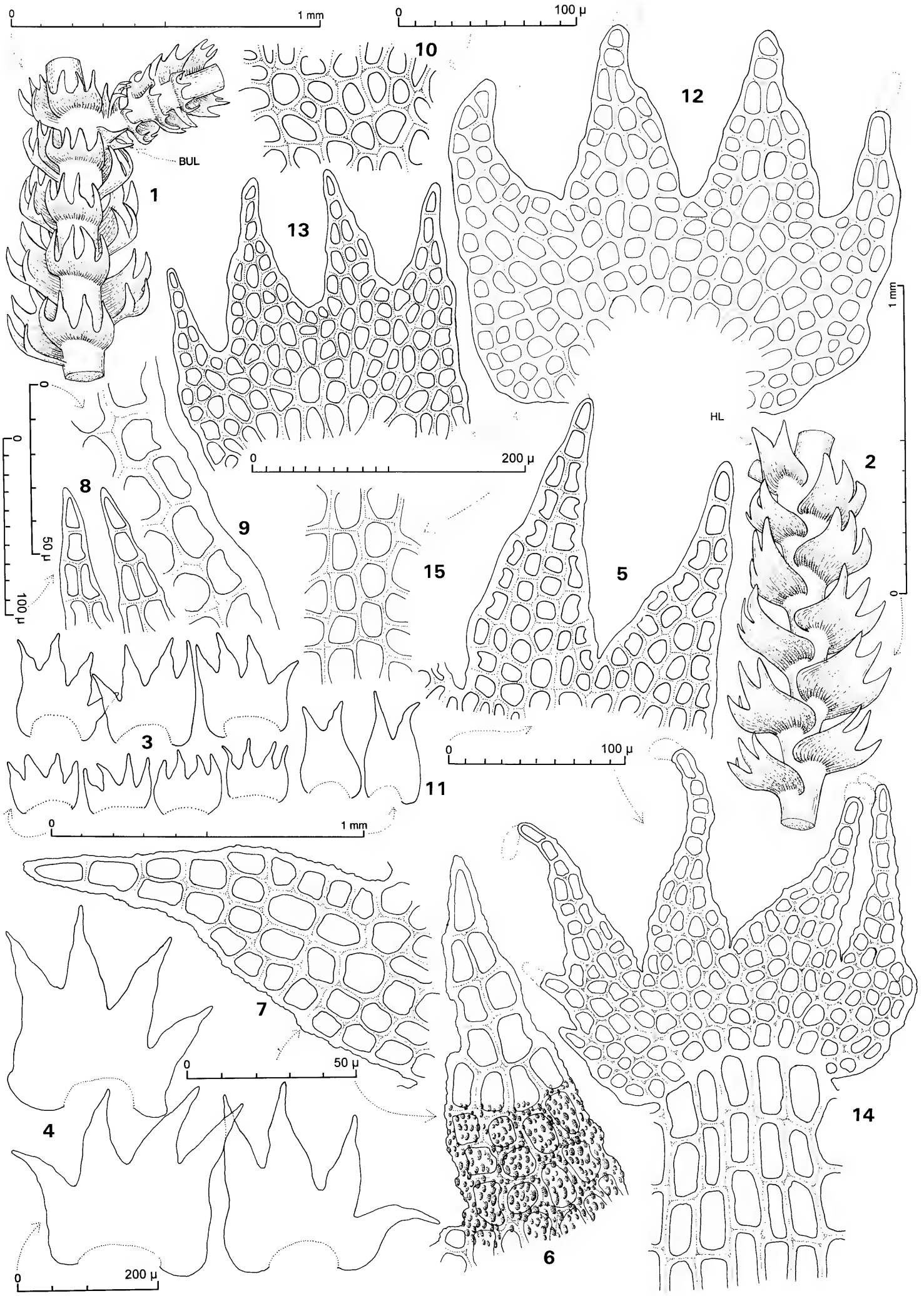

Fig. 40.
Lepidozia novae-zelandiae Steph. 1. Sector of main shoot, and *Frullania*-type branch, ventral view (BUL = first branch underleaf). 2. Sector of main shoot (HL = half-leaf), dorsal view. 3. Leaves, and below, underleaves. 4. Leaves. 5. Dorsal leaf lobes. 6. Dorsal-most leaf lobe, the surface detail indicated in part. 7. Dorsal-most of median leaf lobes, surface detail not shown. 8. Distal sector of dorsal lobes. 9. Portion of dorsal margin of leaf disc. 10. Median cells of leaf disc. 11. Two half-

Lepidozia novae-zelandiae Steph.

[Fig. 40]

Lepidozia novae-zelandiae Steph., Sp. Hepat. 3: 595. 1909 ("Nova Zelandiae"). Lectotype (*fide* Engel and Schuster, 2001): New Zealand, without specific locality, *Colenso 767* (G!).

Plants brittle, prostrate, in loosely interwoven, ± pure mats, the shoots slender, delicately spinescent, stiff and wire-like, with widely spreading branches, green, nitid when dry, the shoots minute. Branching exclusively of *Frullania* type, ± distantly 1-pinnate, the branches often becoming whip-like, flagelliform and microphyllous; secondary branches sporadic; branch half-leaf subsymmetrical, cordate at the base, 2-lobed to ca. 0.4; first branch underleaf (1)2–3(4)-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, nearly aligned with underleaves of branch. Ventral-intercalary branching not seen. Leaves when moist (or dry) moderately concave, with the lobes somewhat incurved, contiguous to ± distant, with much of stem visible in dorsal view, somewhat longer than wide, 0.25–0.3 mm long at longest point, 0.25–0.35 mm wide at widest point, spreading, the insertion subtransverse to weakly incubous; leaves variable, ± symmetric to moderately asymmetric, subequally 4(5)-lobed, the leaves divided to ca. 0.6 (median sinus), in ± symmetrical leaves the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion. Lobes long-acute to short-acuminate, typically somewhat apiculate, the ventral shorter than the dorsal lobes and somewhat divergent, the dorsal lobes 4–5 cells wide at base; lobes terminating in a single cell or in a uniseriate row of 2 cells, the cells of uniseriate row elongated (to 2:1), typically strongly thick-walled, the septa somewhat to distinctly dilated, the terminal cell tapering to a point; surface of lobes coarsely papillose. Disc subsymmetric to obliquely truncate, 6–10 cells high at dorsal sinus, 4–6 cells high at ventral sinus, the margins entire, the dorsal margin ± straight, abruptly cordate near the base, entire to sinuate; ventral margin entire or sinuate, sometimes with an accessory lobe. Cells of disc-middle often strongly thick-walled, occasionally with small to medium trigones, 11–16 μm wide × 14–22 μm long; median basal cells in 1 (locally 2) rows of enlarged cells; marginal cells of disc and lobes with a strongly thickened, often concave outer wall (the wall thickening often crescentic and bulging into the cell lumen), the septa ± dilated; surface of disc finely to distinctly striate-papillose. Underleaves inserted on 4–6 rows of stem cells, spreading, symmetrically 4-fid to ca. 0.5 (median sinus), narrowing to the insertion, the lobes plane, slenderly acuminate, terminating in a single cell or in a uniseriate row of 2–4(5) cells; disc 4–7 cells high at median sinus, the margins plane, entire.

Androecia and gynoecia not seen.

Comments: *Lepidozia novae-zelandiae* is closely allied to *L. laevifolia*, as evidenced by the coarsely papillose leaves (Fig. 40: 6) and by the sinuate leaf margins. It differs in the subtransverse to weakly incubous leaf insertion (Fig. 40: 2), the ± straight dorsal margin (Fig. 40: 2–4), the strongly thickened outer walls and dilated septa of the marginal cells of both disc

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leaves. 12–13. Underleaves, cellular detail. 14. Portion of stem with underleaf; note ventral merophyte width of 5 cells. 15. Ventral cortical cells of stem, surface view. (Figs. 1–3, 5, 8–11, 13, 15, from *Schuster 59645b*, New Zealand, South Is., Westland EP, upper reaches of Haast R., 1 km N of Haast Pass; 4, 6, 7, 14, from *Engel 23107*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, Cross Creek; 12, from *Hodgson s.n.*, New Zealand, North Is., Gisborne EP, Lake Waikaremoana.)

and lobes (Fig. 40: 5–9), the elongated (to 2:1) cells of the uniseriate portion of the lobe apices (Fig. 40: 5–8), and the distinctly thickened stem epidermal cell walls (Fig. 40: 14, 15). *Lepidozia pumila* resembles this species in the ± straight dorsal margin of the leaves and thickened walls of the marginal cells, but the leaf surfaces are typically smooth, and the leaves are more distinctly incubous.

In *Lepidozia novae-zelandiae* the abaxial cell walls of disc and lobes are typically thickened; these thickenings can also be seen by focusing on the ventral margins of the lobes. Similarly thickened cell walls are present in *L. fugax* (Fig. 39: 4, 9), but the characteristic deciduous lobe tips, and the barrel-shaped cells and constricted septa of the uniseriate row, will immediately distinguish that species from *L. novae-zelandiae*.

Three extremes are assigned to this species, which differ as follows.

Key to the varieties of *L. novae-zelandiae*

1a. Leaf lobes, excluding ventral-most, (3)5–6 cells wide, to 7–9 cells long; first branch underleaf (1)2–3(4)-lobed; underleaves with disc 4–5 cells high, the lobes 4–5 cells wide; underleaves inserted on 4–6 cell rows 2

2a. Dorsal leaf sinus descending ca. 0.35–0.4; ventral sinus descending usually over 0.5 the leaf length; dorsal and ventral sinuses usually wide open, V-shaped; leaf lobes apices ending in (1)2 clearly elongated (to 2:1) cells . . . . . var. *novae-zelandiae* (p. 238)

2b. Dorsal leaf sinus descending ca. 0.3–0.35 the leaf length; ventral sinus descending 0.45–0.5; dorsal (and often ventral) sinuses slit-like or narrowly V-shaped; leaf lobe apices ending in (1)2–3 subquadrate to short-triangular cells (1–1.5:1) . . . . . var. *heterostipa* (p. 239)

1b. Leaf lobes 2–3 cells wide, 4–6 cells long; first branch underleaf 1- or 2-lobed; underleaves with disc 2 cells high, the lobes usually few-celled, 2 cells wide at base; underleaves (8 cells wide at base), inserted on 4 cortical cell rows . . . . . var. *minima* (p. 239)

Lepidozia novae-zelandiae Steph. var. ***novae-zelandiae***

Distribution and Ecology: Endemic to New Zealand: Auckland Islands, South Island (540–1050 m), North Island (60–625 m). Known from Southland, Westland, Western Nelson, Volcanic Plateau, Gisborne, Auckland and Northland EPs.

In the South Island the variety is known from few, scattered localities. At Waikaia State Forest (Southland, 260 m) it occurs on bryophyte-covered banks, admixed with *Lepidozia concinna*, in a mature *Nothofagus fusca – N. menziesii* forest. In the Haast Pass area (Westland) on steep, humid but never wet, shaded, vertical, south-facing cliffs in a *N. menziesii* forest with *Plagiochila caducifolia*, *Gymnomitrion cuspidatum*, *Diplophyllum domesticum* and *Radula* sp. Also on clayey vertical banks of a large sinkhole in a *N. menziesii* forest on Mt. Arthur (Mt. Arthur Hut Track, Kahurangi Natl. Park, 1050 m).

In the North Island known from Tongariro Natl. Park within a mixed broadleaf forest (with *Nothofagus menziesii* common); plants grew very loosely over soil on a vertical bank of the Mangawhero River. In the Kaimai Ra. it occurs at 60 m on boulders well above water level in a stream system with several pools and low waterfalls in a mixed broadleaf–podocarp forest, with *Dacry-*

dium cupressinum emergent over a canopy of *Beilschmiedia tawa* and occasional *Weinmannia silvicola*. In the Waipoua area the species occurred on a roadside bank under protective cover, with *Blechnum*, beneath an *Agathis australis* forest. Also known from the Lake Waikaremoana area.

Lepidozia novae-zelandiae var. ***heterostipa*** R.M.Schust.

Lepidozia novae-zelandiae var. *heterostipa* R.M.Schust. *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 70. *f. 25*. 2001. Type: New Zealand, North Is., Tongariro Natl. Park, Tree Trunk Gorge, along west bank of Tongariro River, 15 Feb. 1995, *Schuster 95-772*.

Branching with strongly variable first branch underleaves: on one stem primary underleaves 1-, 2-, and 3-lobed. Leaves usually strongly asymmetrically quadrifid; dorsal lobes separated by a sinus descending usually (0.35)0.4–0.45 the leaf length, the lobes narrow, usually 3–4 cells broad at base; dorsal-most sinus (between the two dorsal lobes) usually narrow, often slit-like. Underleaf bases conspicuously cordate.

Distribution: Endemic to New Zealand and known only from the type.

Lepidozia novae-zelandiae var. ***minima*** R.M.Schust.

Lepidozia novae-zelandiae var. *minima* R.M.Schust. *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 71. 2001. Type: New Zealand, South Is., Fiordland, Falls Creek, *Schuster 48802b*.

Plants rather rigid and wiry, appearing small-leaved (for the stem diam.), the shoots with leaves to ca. 0.7 mm broad. Branching remotely 1-pinnate, the branches short, remote; first basal branch underleaf 1- or 2-lobed. Stem only ca. 6 cells in vertical diam., with lateral merophytes 4–5 cells broad; cortical cells very thick-walled; medulla of strongly thick-walled cells. Leaves only 175–200 μm broad, asymmetrically 4-fid, the median sinus descending ca. 0.55–0.6, deeper than the dorsal sinus (dorsal pair of lobes forming a perceptible, ± parallel-sided pair); disc ca. 4 cells high to dorsal sinus; dorsal lobes only 2–3 cells broad at base, to 4–6(7) cells long, ending in 2(3) single cells that are 1.5–2× as long as broad. Underleaves inserted on 4 rows of cortical cells, small, the disc usually 2 cells high, the lobes 2(3) cells broad at base, (3)4 cells long.

Distribution: Endemic to New Zealand and known only from the type.

Lepidozia acantha J.J.Engel

[Fig. 41]

Lepidozia acantha J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 71. *f. 27*. 2001. Holotype: New Zealand, North Is., Whakarewarewa Thermal Reserve, Sept. 1939, *Hodgson s.n.* (F); isotype: (CHR).

Plants procumbent, in thin mats, slender, flexuous, with spreading branches, pale green, nitid, delicately spinescent when dry, the shoots small to medium, to 1 cm wide (stem to branch extremities). Branching nearly exclusively of *Frullania* type, somewhat irregularly and loosely pinnate, the branches slender, short to elongated and distinctly whip-like, long-flagelliform and microphyllous; secondary branches not seen; branch half-leaf symmetric, linear, bilobed

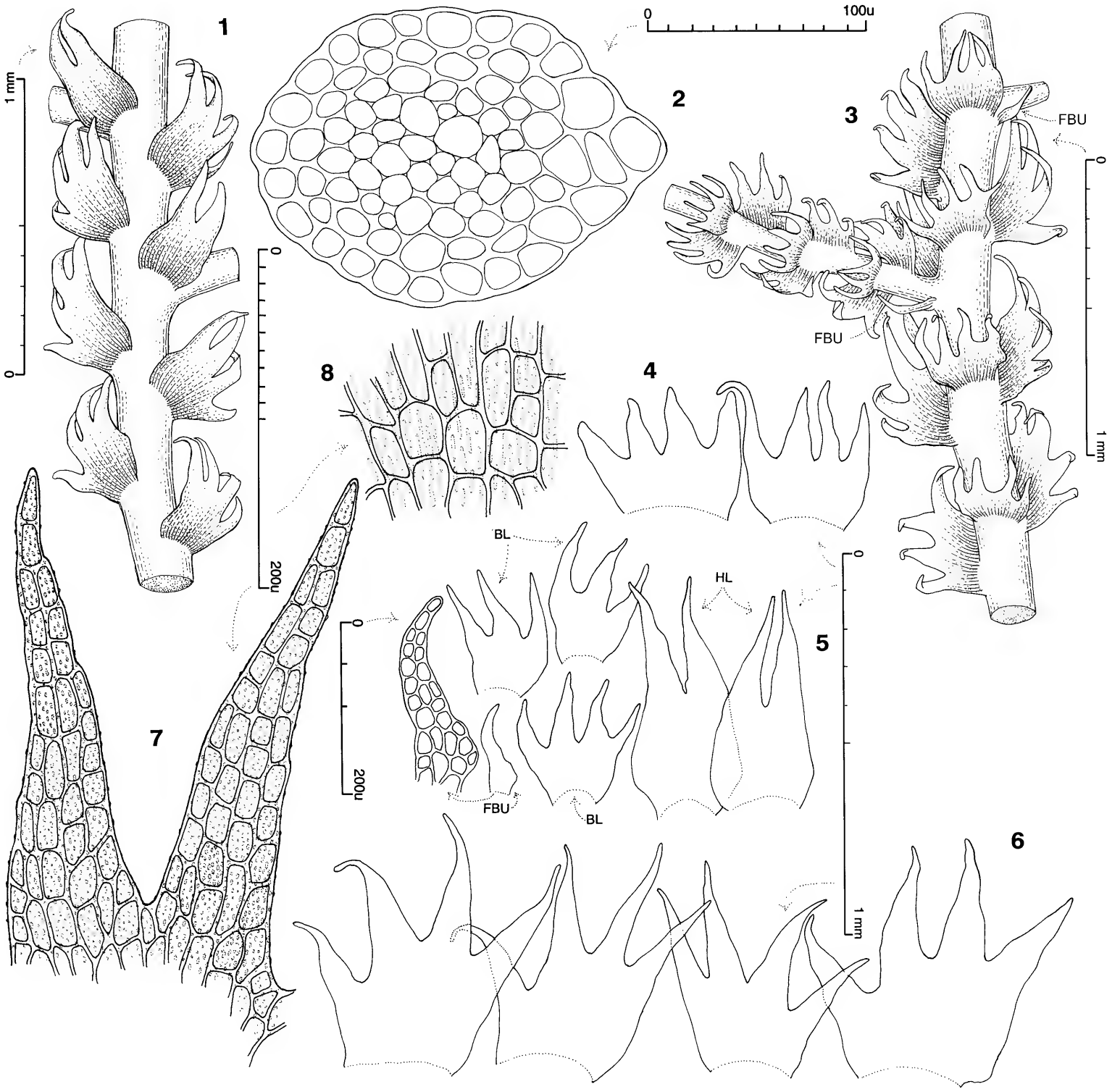

Fig. 41.
Lepidozia acantha J.J.Engel. 1. Sector of main shoot, dorsal view. 2. Stem, cross section. 3. Sector of main shoot with *Frullania*-type branch, ventral view (FBU = first branch underleaf). 4. Underleaves. 5. Half-leaves (= HL), 3- and 4-lobed primary branch leaves (= BL) and, at left, first branch underleaf (= FBU) (cellular detail of first branch underleaf at far left). 6. Leaves. 7. Leaf lobes (surface detail indicated). 8. Median leaf cells (surface detail indicated). (All from type.)

to 0.5; first branch underleaf undivided and subulate, rarely bilobed, inserted on ventral or ventral-lateral face of main axis and aligned with branch underleaves. Ventral-intercalary branches sporadic, leafy. Leaves when dry strongly ventrally secund, with the lobes straight to slightly incurved; leaves when moist strongly spreading, plane or (when lobes slightly incurved) slightly concave, contiguous to distant, with much of stem exposed in dorsal aspect, 0.45–0.65 mm long at longest point × 0.5–0.65 mm wide at widest point, the insertion distinctly incubous; leaves ± symmetric, deeply and subequally 4-lobed, divided to ca. 0.5–0.6 (median sinus), the distance from dorsal sinus base to insertion slightly greater than that from ventral sinus to insertion. Lobes long and narrowly attenuate, subequally divergent, the dorsal

lobe 5–7 cells wide at the base, the ventral lobes similar to the dorsal in size, the lobes terminating in a single cell or more commonly in a uniseriate row of 2–4 cells; cells of uniseriate row somewhat elongated (up to 2.5:1), evenly thick-walled; surface of lobes closely and distinctly short striate-papillose. Disc subsymmetric, subdeltoid, 8–10 cells high at dorsal sinus, 5–8 cells high at ventral sinus, the margins entire, the dorsal margin straight (at most feebly ampliate), the ventral straight. Cells of disc-middle moderately and evenly thick-walled, subquadrate to somewhat longitudinally elongated (particularly those aligned with second lobe), 18–23 μm wide × 27–41 μm long; median basal cells larger, in one to several rows; surface of disc closely striate-papillose, becoming long-striate at disc base. Underleaves inserted on 5–7 rows of stem cells, rather large for plant size, ca. 1–1.5× stem width, plane, spreading, symmetrically quadrifid to ca. 0.5–0.6, the lobes long and slenderly attenuate, ending in a single cell or more often a uniseriate row of 2–3 cells, the cells of uniseriate row quadrate to elongated; disc 4–6 cells high at median sinus; disc margins entire.

Androecia and gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand and known from a limited number of collections. Found at a single South Island station at Camp Creek (Westland, 900 m). North Island populations are from the Rotorua area, at 185 m under *Leptospermum scoparium* and from edges of shaded paths in thermal spring areas, and on a very rotted, decorticated, bryophyte-covered log in a mixed broadleaf–podocarp lowland forest (Pakiri Scenic Reserve, SSE of Mangawhai Heads, Northland, ca. 30 m).

Comments: Resembling *Lepidozia bidens* in the narrowly attenuate lobes, the elongation of uniseriate row cells, and the feebly ampliate dorsal margin. It differs in the distinctly incubous leaf insertion (Fig. 41: 1), the deeply and subequally lobed leaves (Fig. 41: 6), the closely papillose leaf surface (Fig. 41: 7, 8), the larger underleaves with slenderly attenuate lobes, and the smaller size.

The disc surface is closely striate-papillose (Fig. 41: 8), as in *Lepidozia laevifolia* and its var. *acutiloba*. *Lepidozia acantha* differs from the latter in the narrowly attenuate leaf lobes, and from the former in the ± symmetrical leaves, the lobes subequally spreading, the ventral lobes not widely divergent from the paired dorsal lobes.

The species differs from all other New Zealand members of *Lepidozia* except *L. elobata* by the consistently undivided first branch underleaves (Fig. 41: 3, 5). The first branch underleaf is subulate in *L. acantha* vs. rather broad-based and strongly tapered in *L. elobata*. Also, in *L. elobata* the half-leaf is only 0.2–0.25 bifid vs. 0.4–0.45 in *L. acantha*; leaf lobes are much less tapered and their end cells are scarcely elongated. It is notable that undivided first branch underleaves are also found in many *Telaranea* species, as is the presence of 3-lobed branch leaves (Fig. 41: 5); *L. acantha* can be distinguished from superficially similar diminutive *Telaranea* species by the absence of a hyaloderm (Fig. 41: 2), and the papillose surface of the leaves.

Lepidozia elobata R.M.Schust.

Lepidozia elobata R.M.Schust. *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 74. *f. 28*. 2001.
Holotype: New Zealand, North Is., Auckland Harbor, Rangitoto Is., summit area, at tree base, *Schuster 95-401* (F).

Plants creeping, light green, whitish when dry, only feebly nitid when dry, small, the main shoots with leaves ca. 430–640 to 700 μm wide; shoot apices and branch apices decurved,

especially in drying. Branches almost exclusively of *Frullania* type, 1-pinnate, rather irregularly and remotely so, the branches usually of limited length, but sporadic branches elongating and becoming flagelliform; branch leaves normally similar to stem leaves, quadrilobed like them; first branch underleaf inserted in line with succeeding branch underleaves, consistently unlobed, ovate lanceolate to narrowly ovate, ending in a single cell, usually standing stiffly away from stem. Ventral-intercalary branches sporadic, flagelliform. Stems with hyaloderm well developed, the cortical cells rather thin-walled. Leaves adaxially concave, the dorsal lobes decurved/deflexed, the ventral-most lobe usually strongly incurved; leaves of leading stems variable, typically quadrilobed for ca. 0.2–0.25(0.3) dorsally to 0.4–0.45 ventrally, the dorsal lobes usually somewhat smaller than the ventral, the lobes acute but never long-acute, ending in 1 or 2 superposed cells that are not or weakly elongated; some to many leaves almost symmetrically quadrifid, the lobes then subequal but the two outer lobes usually somewhat smaller; leaf at dorsal base at most weakly cordate. Cells in lobes subquadrate, ca. 11–14 × 13–16 μm, in leaf middle scarcely larger; cells of leaf base much larger, rather inflated, 21–30 μm wide × 27–50 μm long, forming a small basal field; surface weakly papillose above, weakly striolate basally. Underleaves inserted on ca. 5 rows of stem cells, standing stiffly away from stem or subsquarrose, under 0.45 quadrifid, the lobes usually 2 cells broad basally. No asexual reproduction. Otherwise unknown.

Distribution and Ecology: Endemic to New Zealand: North Island (150–380 m). Known from Southern North Island (Tararua Ra., Ruahine Ra.) and Auckland (Rangitoto Island) EPs. The Southern North Island collections were both from the vertical sides of boulders 1–2 m above streams.

Comments: *Lepidozia elobata* is part of a complex of small species that includes *L. pumila*, *L. acantha*, *L. novae-zelandiae* and *L. bidens*. It can be separated from all taxa of that complex, except *L. acantha*, by the consistently unlobed first branch underleaves. It is also similar to *L. acantha* in having leaves that do not consistently show a clear division between a pair of dorsal lobes, set off from the ventral lobes. At times the leaf tends to be almost equally quadrifid, although like all *Lepidozia* species, the disc is lower ventrally than dorsally.

Lepidozia elobata is distinct from *L. acantha* in the relatively broad-based, ovate-lanceolate first branch underleaf; the shorter and broader leaf bases, not long-tapered as in *L. acantha*; the subisodiametric cells of leaf lobe apices; the obscurely papillose surface; and the relatively high disc, about as high or higher than the length of the leaf lobes. Also, in *L. acantha* branch leaves are typically trifid; in *L. elobata* they are almost uniformly quadrifid, like main axis leaves.

Lepidozia pumila J.J.Engel

[Fig. 42]

Lepidozia pumila J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 76. *f. 29*. 2001. Holotype: New Zealand, South Is., Fiordland Natl. Park, Moraine Creek, Hollyford Valley, ca. 400–650 ft., *Schuster 48111a* (F); isotype: (CHR).

Plants closely prostrate, flexuous, with spreading branches, green, nitid when dry, the shoots minute to small, 365–490 μm wide (leaf tip to leaf tip), to 5 mm wide, including branches. Branching nearly exclusively of *Frullania* type, rather short, usually irregularly and distantly pinnate to ± regularly pinnate, the primary (and secondary) branches often becoming whip-

like, flagelliform and microphyllous; secondary branches occasional; branch half-leaf subsymmetrical, cordate, 2-lobed to ca. 0.3; first branch underleaf (1)2–4-lobed, inserted on ventral side of branch base to the ventral-lateral side of junction of main axis and branch, in both cases the first branch underleaf aligned with underleaves of branch. *Acromastigum*-type branches (?)occasional. Ventral-intercalary branching occasional, leafy. Leaves cup-shaped (with the tips of the lobes incurved and not visible in dorsal view) to concave, contiguous, with much of stem visible in dorsal view, somewhat longer than wide, (0.25)0.4–0.5 mm long and wide, spreading, the insertion weakly to distinctly incubous; leaves usually strongly asymmetric, 4(5)-lobed, the leaves divided to ca. 0.45–0.55 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion. Lobes attenuate, somewhat apiculate, the dorsal lobes sometimes paired, the two ventral shorter and somewhat divergent from the dorsal lobes, the lobes terminating in a uniseriate row of 2–4 cells, the cells of uniseriate row ± isodiametric or slightly longer than wide, thick-walled; dorsal lobe (2)3–5 cells wide at base; surface of lobes smooth or faintly and indistinctly papillose. Disc asymmetric, obliquely truncate and deltoid, 10–12 cells high at dorsal sinus, 4–6 cells high at ventral sinus, the margins entire, the dorsal margin ± straight, abruptly cordate near the base. Cells of disc-middle evenly and distinctly thick-walled, occasionally with small trigones, 20–33 μm wide and long; median basal cells in 1 (locally 2) rows of enlarged cells; marginal cells of disc and lobes with a thickened outer wall; surface of disc smooth. Underleaves inserted on 5–6 rows of stem cells, spreading, short, broader than high, symmetrically 4-fid to ca. 0.4–0.55 (median sinus), the lobes plane, slenderly acuminate, often only 2–3 cells wide at base, entire, terminating in a uniseriate row of 3–5 cells; disc 4–5(6) cells high at median sinus, the margins plane, entire.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, broadly ovate; apices 2–4-dentate-lobulate, each lobule terminating in a single cell or a uniseriate row of 2 cells; lamina margin bordered by thin to slightly thick-walled cells of variable shape and orientation, the apical or free end of marginal cells slightly divergent and forming a short projection, the margin irregularly and often sparingly crenulate; bracteole similar in size and form. Perianth rather long and prominent, slenderly cylindrical-fusiform, straight, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes crenate-subdenticulate.

Seta with 8 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule oblong, the wall 38–41 μm thick, of 3 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and several large nodule-like to spine-like thickenings alternating with those that are devoid of thickenings (or are rarely locally thickened), the transverse walls usually devoid of thickenings or sporadically with an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete.

Spores 13.9–14.9 μm in diam., the wall brown, with dense, rather coarse but low, sharply defined papillae and simple or furcate vermiculate markings. Elaters rigid, nontortuous, 7.7–9.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.4–3.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands, South Island (100–1525 m), North Island (ca. 400–1080 m), Chatham Islands. Known from Fiordland, Southland, Otago, Westland, Canterbury, Marlborough (Branch River), Volcanic Plateau (Tongariro Natl. Park), Taranaki (Pukeiti Bush) and Gisborne (Lake Waikaremoana) EPs.

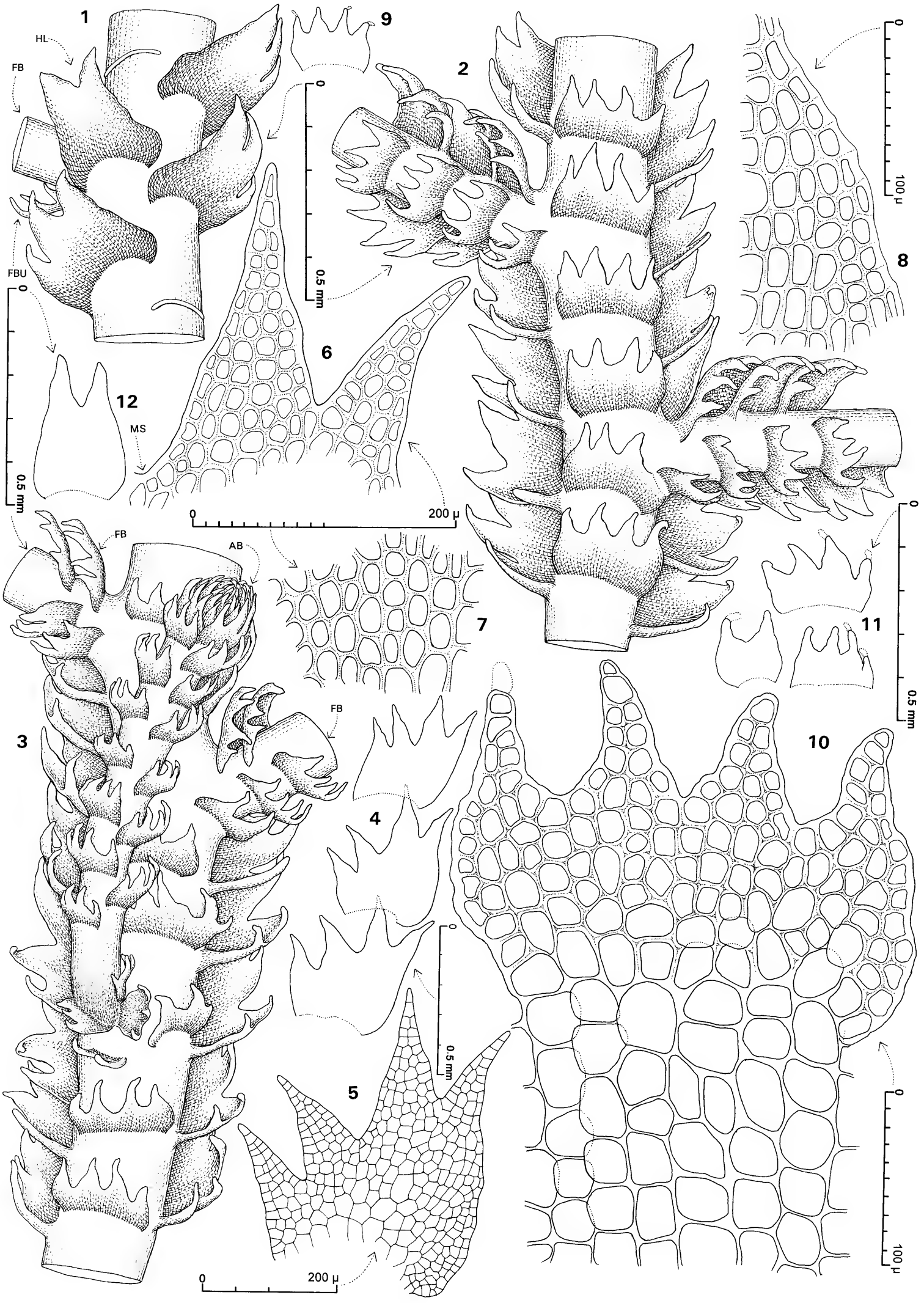

Fig. 42.
Lepidozia pumila J.J.Engel. 1. Portion of main shoot with *Frullania*-type branch (= FB; HL = half-leaf; FBU = first branch underleaf), dorsal view. 2. Portion of main shoot with 2 *Frullania*-type branches, ventral view. 3. Portion of main shoot with *Acromastigum*- (= AB; note half-

A species occurring over a broad elevational gradient. It occurs in forests ranging from 570 m to the upper reaches of the forest and found corticolous or on shaded, moist cliff faces and boulders. It ranges up to 1370 m in the penalpine zone on rock (particularly with some soil accumulation) or in rock crevices. Occasionally in lower-elevation forests (100–200 m) over wet humus of the shaded forest floor, and then occurring with *Lepidozia pendulina* or on the caudex of *Dicksonia squarrosa*.

Comments: This smallest New Zealand member of the *laevifolia* group is evidently rather rare. Suboptimal expressions of *Lepidozia laevifolia* with poorly developed surface papillae may well be mistaken for this species. For further details, see the discussion under *L. laevifolia*.

A minute phenotype of the species occurs in median and upper elevations on cliff faces and boulders and forms pure, tight, compact mats of usually wire-like, upright shoots. Shoots are ca. 350–400 μm (not including branches), and leaves are minute (400–500 μm wide and long) and in dry plants quite inconspicuous. Despite their seemingly impoverished condition, these specimens bear mature perianths.

Lepidozia bidens J.J.Engel

[Fig. 43]

Lepidozia bidens J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 79. *f. 30*. 2001. Holotype: New Zealand, South Is., Nelson/Westland Prov. boundary, Paparoa Ra., S side of Pororari River, upriver from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel 19204 – c. per.* (F); isotype: (CHR).

Plants procumbent, in thin mats, slender, flexuous, with spreading branches, pale green, nitid, delicately spinescent when dry, the shoots small to medium, to 1.5 cm wide (stem to branch extremities). Branching exclusively of *Frullania* type, regularly pinnate, the branches slender, short to greatly elongated and distinctly whip-like, long-flagelliform, microphyllous; secondary branches sporadic to occasional; branch half-leaf symmetric, linear (at times slightly broadening toward base), 2(rarely 3)-lobed to 0.3–0.45; first branch underleaf (2)3–4-lobed, inserted on ventral side of branch base or at juncture of branch and main axis, aligned with branch underleaves. Ventral-intercalary branches not seen. Leaves when dry slightly concave, with the tips of the lobes straight to slightly and broadly incurved; leaves when moist spreading, slightly concave, contiguous to distant, with much of stem exposed in dorsal aspect, 0.45–0.5 × 0.35–0.5 mm, the insertion subtransverse to weakly incubous; leaves distinctly asymmetric, unequally 4(5)-lobed, divided to ca. 0.5–0.65 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion. Lobes long and narrowly attenuate (the dorsal lobes especially so), the dorsal lobes parallel to somewhat divergent (rarely approaching 90°), ± distinctly paired, 3–5 cells wide at base, the ventral lobes often shorter, curved and spreading (often at right angles to the dorsal margin), the lobes

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underleaf) and *Frullania*-type (= FB) branches, ventral view. 4. Three leaves. 5. Leaf, cellular detail. 6. Dorsal pair of leaf lobes (MS = median sinus). 7. Median disc cells. 8. Marginal cells of dorsal margin of disc showing thickened free wall. 9. Underleaf (at same scale as fig. 4). 10. Portion of stem with underleaf; note ventral merophyte width of 6 cells. 11. First branch underleaves. 12. Half-leaf. (All from type.)

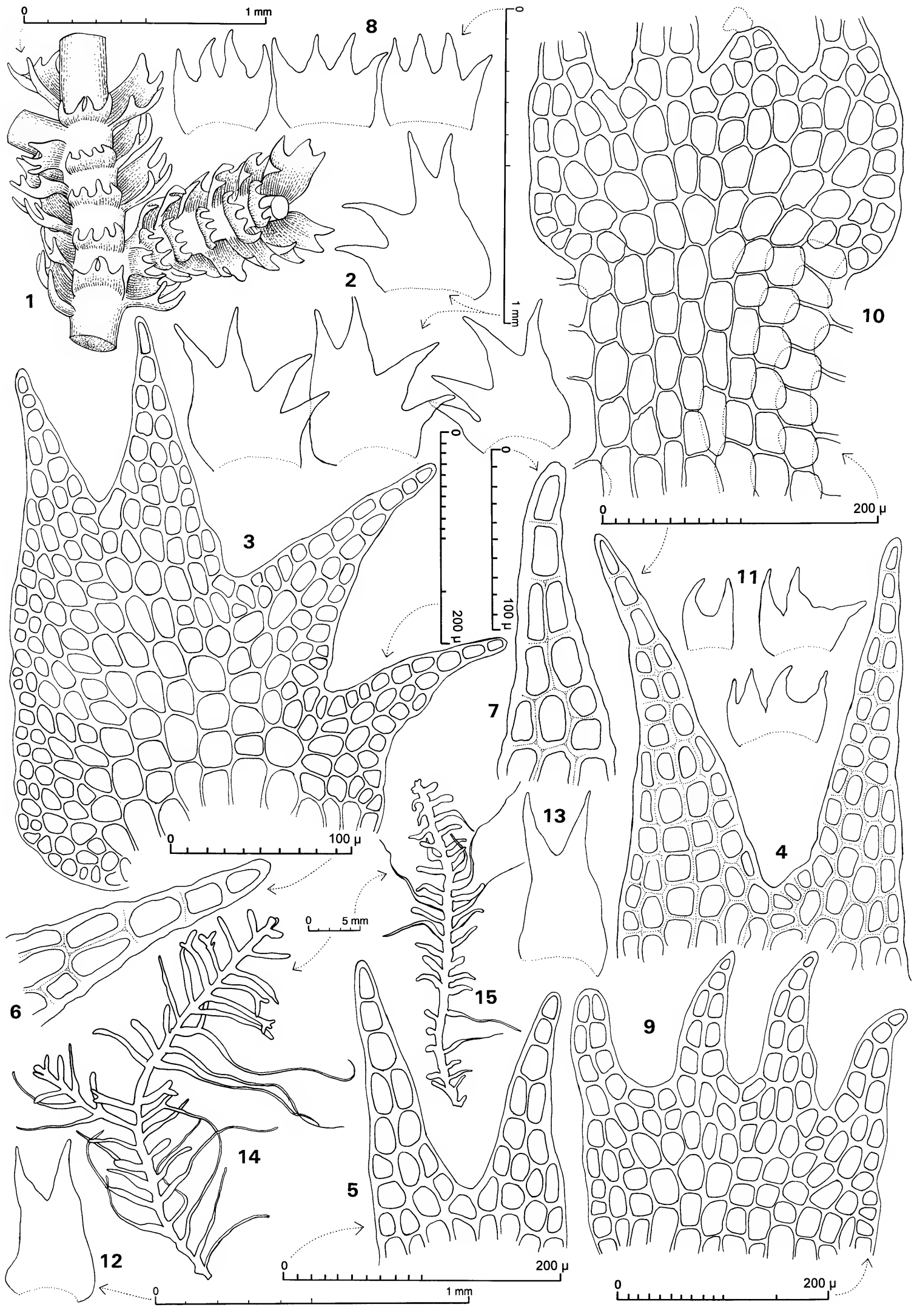

Fig. 43.
Lepidozia bidens J.J.Engel. 1. Sector of main shoot with *Frullania*-type branch, ventral view. 2. Leaves. 3. Leaf. 4, 5. Dorsal pairs of leaf lobes. 6, 7. Dorsal lobes. 8. Underleaves. 9. Underleaf. 10. Portion of stem with underleaf; note ventral merophyte width of 8 cells. 11. Two-, 3- and 4-

terminating in a uniseriate row of 2–3 cells; cells of lobes and uniseriate row somewhat elongated (up to 2:1, but the terminal 1–2 cells sometimes subquadrate), evenly thick-walled; surface of lobes smooth to faintly striate-papillose. Disc strongly asymmetric, subdeltoid, 8–10 cells high at dorsal sinus, 4–5 cells high at ventral sinus, the margins entire, the dorsal margin straight (at most feebly ampliate). Cells of disc-middle moderately and evenly thick-walled, ± longitudinally elongated, particularly those in the dorsal half of leaf, 18–31 μm wide × 30–50 μm long; median basal cells distinctly larger, in 1 to several rows; marginal cells of disc and lobes with a thickened outer wall; surface of disc smooth to faintly striate-papillose. Underleaves inserted on 8 rows of stem cells, small, ca. 1–1.1× stem width, plane, strongly spreading to squarrose, symmetrically quadrifid to ca. 0.4–0.5, the lobes attenuate, ending in a single cell or a uniseriate row of 2–3 cells, the cells of uniseriate row often elongated; disc 4–6 cells high at median sinus; disc margins entire.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, narrowly ovate to suborbicular; apices with 2–4 short, irregular lobes, the lobes crenate-denticulate to spinose-dentate; lamina margin bordered by cells of variable shape, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate to the base; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth; mouth cells thick-walled, especially at the summit, at the apical end laterally free for varying lengths, the mouth thus crenate-denticulate.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (35–330 m), North Island (ca. 400–920 m). Known from Otago (Dunedin), Westland, Western Nelson, Volcanic Plateau, Taranaki and Gisborne EPs.

A forest plant of both South and North islands. In the South Island it occurs in wet, rich, lower-elevation forests (0–330 m) in banks of bryophytes or it may be corticolous (on, for example, *Fuchsia*). It also may occur in open forests (again, below 330 m) of, for example, *Nothofagus fusca* and *Dacrydium cupressinum*, and here occurs in large masses at tree bases. In the North Island it occurs, for example, on rotted, decorticated, bryophyte-covered logs in the mature podocarp forest at Whirinaki Forest Park. The species reaches higher elevations in the North Island, occurring on bryophyte-covered wood in *Nothofagus – Dacrydium cupressinum – Podocarpus totara* forests at Waikareiti Track (Urewera Natl. Park, 920 m), and at Waipai Swamp (also Urewera Natl. Park, 720 m) on the sides of old *Sphagnum* mounds in a low, open, boggy area with *Sphagnum* hummocks, *Leptospermum scoparium* and *Dracophyllum subulatum*.

Comments: The species may be immediately distinguished by the distinctly paired, long, narrowly attenuate, dorsal lobes which lend a delicately spinescent appearance to dried plants (Fig. 43: 3–5). Related to this feature is the distinctive appearance of the half-leaves, which

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lobed first branch underleaves (drawn to same scale as fig. 8). 12, 13. Half-leaves (3). 14, 15. Outlines of 2 shoots at low magnification. (Fig. 1, from *Engel 19280*, New Zealand, Western Nelson EP, Paparoa Ra., N side of Tiropahi R.; 2, 3, 5–11, 15, from type; 4, 12–14, from *Child 358*, New Zealand, South Is., Westland EP, Fox Glacier.)

are linear and deeply divided (up to 0.5) (Fig. 43: 12, 13). The ventral lobes are typically shorter than the dorsal, curved and spreading, often at nearly right angles to the dorsal margin (Fig. 43: 2, 3). The species also has distinctive areolation: median cells of the disc are often elongated, particularly in the dorsal half of the leaf, and the median basal cells are larger in contrast to those along the dorsal and ventral margins (Fig. 43: 3).

Lepidozia bidens belongs to a complex of small to minute species that includes *L. novae-zelandiae*, *L. acantha* and *L. laevifolia*, but differs from all three in its regularly pinnate branching (Fig. 43: 14, 15) and generally larger size.

Sect. ***Kirkii*** R.M.Schust.

Lepidozia sect. *Kirkii* R.M.Schust., Beih. Nova Hedwigia 118: 197. 2000. Type: *Lepidozia kirkii* Steph.

Lepidozia kirkii Steph.

[Fig. 50: 1, oil-bodies, p. 268]

Lepidozia kirkii Steph., Sp. Hepat. 3: 598. 1909. Type: New Zealand, South and North Is., *Krone*, *Beckett*, *Kirk* (*non vidi*).

Lepidozia dentifolia Steph., Sp. Hepat. 3: 599. 1909, *syn. fide* Engel and Schuster (2001). Type: New Zealand, Jacksons Track, *Goebel* (G!).

Plants ascending, rather flexuous, with ventrally secund branches, pale green, the shoots medium, to 2 cm wide, including branches. Branching mostly of *Frullania* type, regularly pinnate, the primary branches often becoming whip-like, flagelliform, microphyllous, and rooting in the substrate; secondary branches occasionally present; branch half-leaf ± symmetric to slightly asymmetric, broadly ovate, shallowly 2(3)-lobed to 0.3, irregularly toothed nearly to the base; first branch underleaf 4(5)-lobed, inserted on ventral to ventral-lateral side of branch and aligned with underleaves of branch. Ventral-intercalary branching rare and sporadic, leafy. Stems soft, flexuous, the cortical cells in 1 layer of thick-walled cells somewhat larger than the medullary cells; medullary cells thick-walled. Leaves rigid, concave, with incurved lobes, imbricate and completely hiding stem in dorsal view, 0.6–0.95 mm long at longest point, 0.8–1.4 mm wide at widest point, patent, the insertion distinctly incubous and slightly recurved at dorsal end; leaves distinctly asymmetric, unequally 4-lobed, the leaves divided to ca. 0.4–0.55 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion. Lobes of differing shape, the dorsal pair of lobes acute, the ventral lobe narrowly acuminate to sublinear, the dorsal pair of lobes partially united, the lobes entire or sometimes with 1 to several short teeth, the dorsal lobe 9–14 cells wide at base, the lobes terminating in a single cell or a uniseriate row of 2–3 cells (the ventral often somewhat longer); cells of uniseriate row ± isodiametric to slightly longer than wide, thick-walled. Disc distinctly asymmetric, 22–27(30) cells high at dorsal sinus, 10–14 cells high at ventral sinus; dorsal margin broadly ampliate, the dorsal margin and the confluent margin of dorsal lobe irregularly (often doubly) dentate or serrate (erose) by teeth of 1 to several cells (the margin at times with a few weak teeth); ventral margin entire or sometimes with a process. Cells of disc-middle evenly thick-walled, ± isodiametric to longitudinally elongate, 14–22 μm wide × 18–30(36) μm long; median basal cells enlarged, in 1–2 rows, with irregu-

larly thickened walls; surface smooth to indistinctly striate-papillose. Oil-bodies in upper sector of disc 1–3(5) per cell, hyaline, finely botryoidal, the spherules somewhat projecting beyond membrane, the oil-bodies spherical and 3–4 μm in diam. or irregularly ellipsoidal, sometimes slightly crescent-shaped, with acute tips and 3 × 5.5–7 μm; basal cells with 4–7(9) oil-bodies per cell, more strongly papillose, spherical and 4–5 μm in diam. or ca. 4 × 10 μm and similar in shape as midleaf oil-bodies. Chloroplasts very small. Underleaves spreading, symmetrically 4-fid to ca. 0.45–0.6 (median sinus), the lobes incurved, ± parallel, gradually attenuate, entire or with a tooth or spine, usually blunt at the tip or terminating in a single cell or short uniseriate row of 2–3(5) cells; disc 10–15 cells high at median sinus, disc margins somewhat reflexed, on each side with a lobe-like process distally, the underleaves then appearing 6-lobed.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches mostly from main shoot and occasionally from primary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.3–0.4, the lobes acute; antheridial stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, broadly ovate; apices with 4 short, ± regular lobes, the apical end of the marginal cells often diverging and forming a tooth, the lobes thus crenate-denticulate; lamina margin bordered by thin-walled cells of variable shape and orientation, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate (+ slime papillae) to the base; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed, somewhat contorted mouth, the lobes composed of cells that at the apical end are laterally free for varying lengths, the lobes thus crenate-denticulate.

Seta with 10–14 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule ellipsoidal to oblong, the wall 52–54 μm thick, of (4)5 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and several large nodules alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls usually devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells ± tiered, narrowly rectangular, semiannular bands common, close and numerous, sometimes incomplete.

Spores 14.4–15.8 μm in diam., the wall brown, with coarse, high, sharply defined, widely spaced papillae and simple or furcate vermiculate markings that sometimes coalesce (but do not delimit areolae). Elaters rigid, nontortuous, 9.6–11.5 μm wide, only slightly tapering toward tips, bispiral, the spirals 3.4–3.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands (15 m), Stewart Island (5–530[1280] m), South Island (90–1100 m), North Island (ca. 400–1280 m). Known from Fiordland, Westland, Western Nelson, Volcanic Plateau, Taranaki and Auckland (Coromandel Forest Park) EPs.

The species occurs in forests over a variety of substrates (rock, tree bark, rotten logs, epiphytic on *Weinmannia racemosa*) over a broad altitudinal range (ca. 30–1280 m). It is present in the upper limits of *Nothofagus menziesii* forests, as well as in *N. solandri* var. *cliffortioides* and *W. racemosa – Metrosideros umbellata* forests. In forested sites it occurs with *Goebeliella cornigera*, *Lepicolea scolopendra*, *Lepidolaena taylorii* and *Bazzania adnexa*. It also extends to the upper reaches of the penalpine zone (Kelly Ra., Arthur's Pass Natl. Park, 1040–1110 m)

where it forms tufts on rock. In the southern sectors of South Island it occurs at 100 m or lower. On Stewart Island it occupies a broad altitudinal range. At Belltopper Falls, Port Pegasus, the species may be found on vertical rock faces at ca. 5 m in an open, humid niche dominated by bedrock, with a forest margin of *W. racemosa* and *Dracophyllum*. On the Mt. Rocky summit area it occurred at 530 m deep in a shaded, protected niche under tussock cover in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs, and dwarf heaths to 0.5 m tall that are dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus*.

In the North Island it may be found in forests dominated by *Nothofagus solandri* var. *cliffortioides* (along a small stream, Blyth Track, Tongariro Natl. Park, ca. 1230 m) or in open forests dominated by *Weinmannia racemosa*, *Kunzea ericoides* and *Agathis australis*, and occurs over bare rock of cliff faces (near summit of Table Mtn., Coromandel Forest Park, 820 m). Also near the summit of "Little Moehau" (Coromandel Forest Park, ca. 840 m) on sheltered, vertical banks or on upper branches of stunted *W. silvicola* in a narrow valley system, truncated, sheltered and protected with stunted *W. silvicola*, *Coprosma foetidissima* and *Corokia buddleioides*.

Species found with *Lepidozia kirkii* are *Acrobolbus concinnus*, *Acrochila biserialis*, *Acromastigum colensoanum*, *Bazzania adnexa*, *Breutelia elongata*, *Clandarium xiphophyllum*, *Cuspidatula monodon*, *Dendroligotrichum dendroides*, *Dicranoloma billardierei*, *Goebeliella cornigera*, *Heteroscyphus billardierei*, *H. menziesii*, *Jamesoniella kirkii*, *Kurzia hippuroides*, *Lepidozia obtusiloba*, *L. ulothrix*, *Paraschistochila tuloides*, *Pseudocyphellaria homeophylla* and *Schistochila monticola*.

Comments: The dorsal margin of the leaf disc and the confluent margin of the dorsal lobe are typically coarsely and irregularly (often doubly) dentate or serrate, rather than armed with discrete spines (terminating in a uniseriate row of 2 or more cells) as in *Lepidozia hirta* (Fig. 44: 2, 4, 10). Presence of teeth, even when few in number, will distinguish the species from *L. hirta*. *Lepidozia hirta* also differs in the more deeply lobed underleaves with the lobes often variously and irregularly dissected. The species differs from *L. serrulata* by the acute dorsal pair of leaf lobes, each with a uniseriate row of 2–3 cells and the 1-pinnate branching.

Lepidozia hirta Steph.

[Fig. 44]

Lepidozia hirta Steph., Sp. Hepat. 3: 599. 1909. Type: New Zealand, without specific loc., *Kirk* (G!).
Lepidozia angelii Gottsche *ex* Steph., Sp. Hepat. 3: 596. 1909. Type: New Zealand, without specific loc., (*Angel*) (G!).

Plants delicate, loosely procumbent, rather flexuous, soft and plumose, with weakly ventrally secund branches, pale green, the shoots medium, to 1.7 cm wide, including branches. Branching mostly of *Frullania* type, closely and regularly pinnate, primary branches becoming whip-like, flagelliform, microphyllous, and rooting in the substrate; secondary branches rarely present; branch half-leaf ± symmetric to slightly asymmetric, broadly ovate, shallowly 2-lobed, ± regularly spinose-dentate nearly to the base; first branch underleaf 4(5)-lobed, inserted on ventral to ventral-lateral side of branch and ± aligned with underleaves of branch. Ventral-intercalary branching occasional, stoloniform. Stems rather soft, flexuous. Leaves

rigid, concave, with incurved lobes, imbricate and nearly or completely hiding stem in dorsal view, 0.4–0.5 mm long at longest point, 0.6–0.8 mm wide at widest point, patent, the insertion distinctly incubous and feebly recurved at dorsal end; leaves distinctly asymmetric, unequally 4-lobed, the leaves divided to ca. 0.4–0.65 (median sinus), the distance from dorsal sinus base to insertion greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes of differing shape, the dorsal pair of lobes acuminate, the ventral lobe attenuate, often spreading as a claw, the dorsal lobes not noticeably paired, the lobes entire or with a single prominent spine or with a few small, often opposing teeth, the dorsal lobes (5)9–11 cells wide at base, terminating in a uniseriate row of 2–3(6) cells (the ventral often somewhat longer); cells of uniseriate row ± isodiametric to somewhat longer than wide (2:1 or less), not noticeably longer than basal cells in lobe, thick-walled. Disc weakly asymmetric, 10–16 high at dorsal sinus, 5–8 cells high at ventral sinus; dorsal margin broadly curved to subampliate, the dorsal margin and the confluent margin of the dorsal lobe ± regularly spinose-dentate with 3–6 discrete, short, acuminate, often curved, multicellular spines (the margin often also with several few-celled teeth); ventral margin entire. Cells of disc-middle thick-walled, ± isodiametric to elongate, 12–18 μm wide × 18–25 μm long; median basal cells enlarged, in 1–2 rows, with trigones and irregularly thickened walls; surface striate-papillose. Oil-bodies at midleaf 2–4(5) per cell, moderately botryoidal, colorless, mostly spherical and appearing like blackberries, 3.5–4.5 μm in diam., occasionally citron-shaped with rounded-acute tips and 4–5 × 8–9 μm; basal cells with (3)5–7 oil-bodies per cell, moderately botryoidal but with spherules more strongly protruding beyond membrane. Underleaves spreading, symmetrically 4-fid to ca. 0.55–0.8 (median sinus), the lobes broadly incurved, somewhat divergent, narrowly attenuate, variable: entire to variously and irregularly dissected (with one to several lobuliform spines), the lobes terminating in a uniseriate row of 3–6 cells; disc 6–9 cells high at median sinus, disc margins on each side with a lobe-like spine, the underleaves then appearing 6-lobed.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave to canaliculate, ovate to suboblate; apices with 2–4 teeth or short, irregular lobes or unlobed, the lobes or bract summit crenate-denticulate; lamina margin bordered by thin-walled cells of variable shape and orientation, the apical or free end of marginal cells variously divergent and forming a short projection or tooth, the margin irregularly and at times sparingly crenate-denticulate to the base; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly 3-plicate toward mouth, the perianth gradually narrowing toward the distinctly contracted, obscurely ca. 6-lobulate mouth, the lobules composed of thick-walled cells that at the apical end are laterally free for varying lengths, the lobules thus irregularly crenate-denticulate.

Seta with 9 rows of outer cells surrounding an inner core of numerous much smaller cells. Capsule oblong, the wall 50–53 μm thick, of 4 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and several low, broad nodules alternating with walls that are devoid of thickenings, the transverse walls usually devoid of thickenings or sporadically have 1–2 isolated nodules; innermost layer of cells ± tiered, narrowly to rather broadly rectangular, the longitudinal walls with nodular to spine-like thickenings, and, often, somewhat sinuous sheet-like thickenings, semiannular bands sporadic.

Spores 38.4–42 μm in diam., the wall yellow-brown, thin, with low, dense, close papillae and short, sometimes branched, vermiculate markings that sometimes coalesce but do not

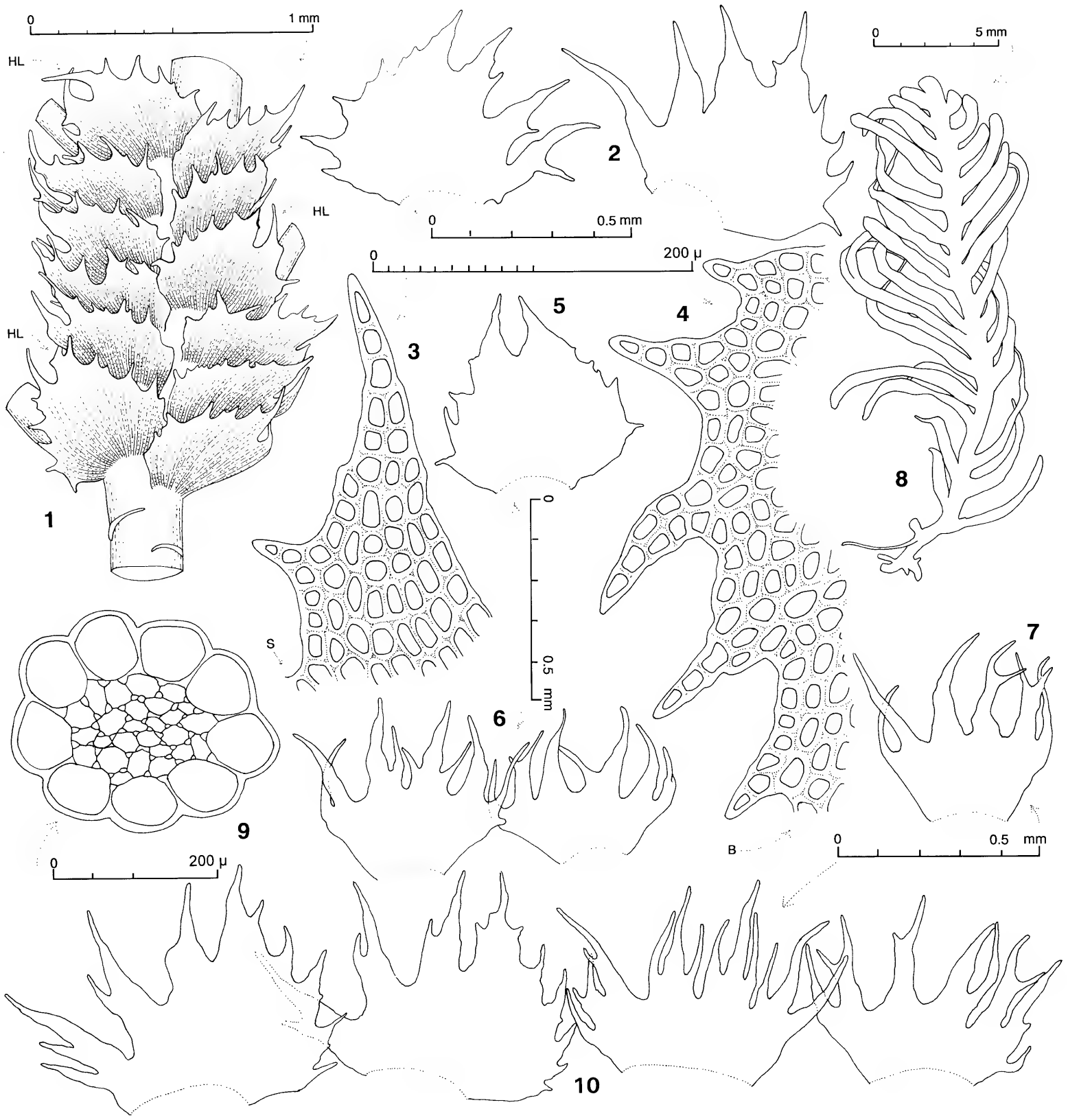

Fig. 44.
Lepidozia hirta Steph. 1. Sector of main shoot, dorsal view (HL = half-leaf). 2. Leaves. 3. Dorsal-most lobe of leaf (S = sinus). 4. Dorsal margin of leaf (B = leaf base). 5. Half-leaf. 6, 7. Underleaves. 8. Outline of plant at low magnification. 9. Seta, cross section. 10. Two leaves and, to right, 2 underleaves, all at same scale. (Figs. 1–8, from *Engel 19205*, New Zealand, South Is., Westland EP, Paparoa Ra., S side of Pororari R.; 9, from *Hatcher 136*, New Zealand, South Is., Canterbury EP, Mt. Torlesse; 10, from *Braggins 94/241*, New Zealand Northland EP, SE corner of Waipoua Forest.)

delimit areolae. Elaters rigid, nontortuous, 24–30 µm wide, only slightly tapering toward tips, bispiral, the spirals 9.6–10.8 µm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (300–600 m), North Island (700–1065 m). Known from Canterbury (Torlesse Ra.), Western Nelson (Paparoa Ra.), Volcanic Plateau (Paeroa Ra., Taupo, Tongariro Natl. Park) and Gisborne (Urewera) EPs.

Occurring in a variety of niches. It is present, for example, at the edges of rills in the pen-alpine zone in areas with mostly snow tussock, but with some *Dracophyllum longifolium*, *Celmisia* and *Empodisma minus*. Also in a low *Nothofagus solandri* var. *cliffortioides* forest with steep, moist, peaty, mossy banks (Mangawhero River), as well as on very old logs in an upper-elevation forest (Paeroa Ra.). At Waipoua Forest the species occurs over rotted wood in a very wet *Weinmannia silvicola – Syzygium maire* forest. It is sometimes epiphytic on tree trunks (recorded from *Nothofagus solandri*, *N. fusca*, *N. truncata* and *Elaeocarpus hookerianus*). Accompanying species are *Acrochila biserialis*, *Bazzania adnexa*, *B. nitida*, *Chandonanthus squarrosus*, *Cuspidatula monodon* and *Hypnum chrysogaster*.

Comments: *Lepidozia hirta* differs from *L. ulothrix* in its smaller leaves and in its closely and regularly pinnate branching (Fig. 44: 8), the branches often becoming whip-like and rooting in the substrate. Typically, *L. ulothrix* is a more robust plant, with distant, abbreviated, somewhat curved branches, and is never epiphytic whereas *L. hirta* is sometimes an epiphyte.

For comments distinguishing this species from *Lepidozia kirkii* and *L. ulothrix*, see under those species.

Lepidozia serrulata J.J.Engel

[Fig. 45]

Lepidozia serrulata J.J.Engel, J. Hattori Bot. Lab. 96: 273. *f. 1*. 2004. Holotype: New Zealand, Stewart Is., Rakiura Natl. Park, Mt. Rocky summit area, 530 m, *Engel, von Konrat & Braggins 24293* (F); isotype: (AK).

Plants loosely prostrate, rather rigid, the hair-like leaf tips lending dried plants a subhoary aspect, pale yellow-green, the shoots medium-sized, to 1.7 cm wide, including branches. Branching nearly exclusively of *Frullania* type, regularly and rather densely 2-pinnate, the branches, particularly the secondary ones, ventrally secund, both at times abruptly becoming flagelliform and whip-like; branch half-leaf subsymmetric (the dorsal margin a little dilated), ovate, 2-lobed, the dorsal margin sparingly and irregularly denticulate-dentate, at times with a few spinose teeth, the ventral margin with a few, stronger, spinose teeth; first branch underleaf 3–4-lobed, inserted on juncture of branch base and main shoot and aligned with underleaves of branch, asymmetric, the sinuses of unequal depth. Ventral-intercalary branching occasional, short, leafy or flagelliform. Stems rather soft and flexuous, the cortical cells in 1 layer of thick-walled cells that are slightly larger than medullary cells; medullary cells distinctly firm-walled. Leaves rigid, fragile, strongly concave, imbricate and nearly or completely hiding stem in dorsal view, 0.9–1.1 mm long at longest point, 0.8–1.1 mm wide at widest point, obliquely spreading, the insertion distinctly incubous, not or slightly recurved at dorsal end; leaves distinctly asymmetric, unequally 4-lobed, the leaves divided to ca. 0.5–0.55(0.7) (median sinus), the dorsal lobes subparallel, the 2(3) ventral lobes moderately divergent, the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion, the dorsal lobes perceptibly to distinctly paired, the dorsal-most sinus often notably shallower, the remaining sinuses then becoming gradually deeper ventrally. Lobes of differing shape, the dorsal pair of lobes caudate, the third lobe subcaudate to sublinear, the ventral-most lobe linear to attenuate, the lobes typically entire, occasionally with 1 small tooth or spine, the dorsal lobes 9–13 cells wide at base, the ventral lobe 6–13 cells wide at base, the lobes terminating in a uniseriate row of (3)4–7(8) cells; cells of uniseriate row moderately elongated

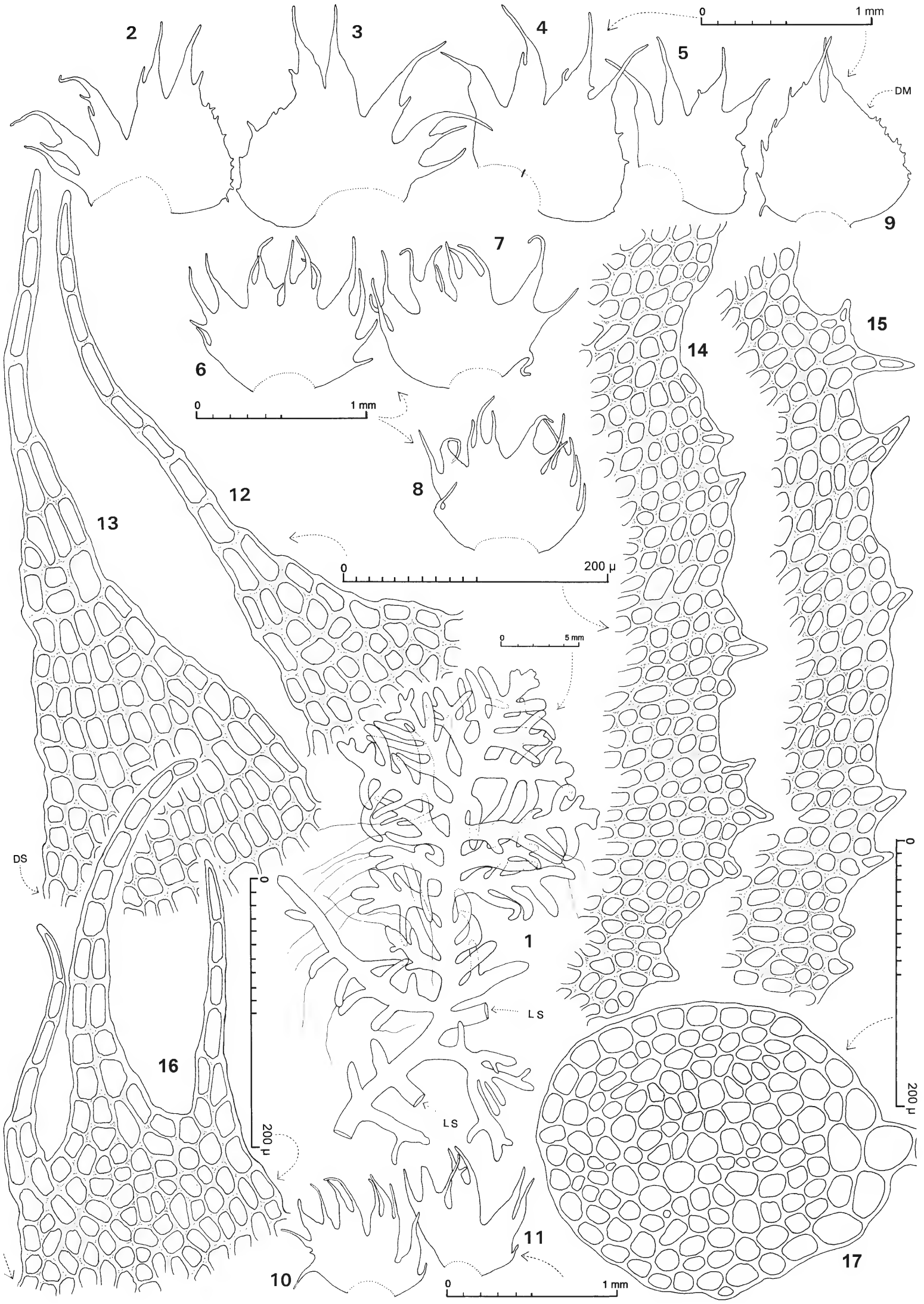

Fig. 45.
Lepidozia serrulata J.J.Engel. 1. Cladograph; the single lines indicate flagelliform sectors of branches (LS = leading shoot). 2–5. Four leaves. 6–8. Underleaves. 9. Half-leaf (DM = dorsal

(2.3–4.3[5.3]:1), thick-walled and with the septa thickened and swollen, the tip cell thickened at the summit. Disc distinctly asymmetric primarily due to strong dilation of dorsal sector, the disc 19–25 cells high at dorsal sinus, 7–12 cells high at ventral sinus; dorsal margin sparingly and irregularly denticulate-dentate, at times with a few small spinose teeth, the teeth often composed of only 1–2 cells; ventral margin much shorter than the dorsal, entire or occasionally with a lacinia, which if especially well developed makes the leaves appear 5-lobed. Cells of disc-middle evenly thick-walled, slightly to moderately elongated, 14–24 μm wide × 28–34 μm long, tending to occur in ± regular longitudinal files; cells in the ampliate sector ± isodiametric, 16–22 μm wide and long; median basal cells enlarged and forming an ill-defined field; surface finely striate-papillose. Underleaves 1.5–2× stem width, spreading, symmetrically basically 4-fid to 0.5 (median sinus), the lobe base tapering distally or ± parallel-sided, 11–15 cells wide at extreme base, the distal portion acuminate-subcaudate, the lobes with 1–2 accessory, at times opposed, teeth or cilia that are always smaller than the lobe, the distal sector terminating in a single cell or a uniseriate row of 2–6 cells; disc 11–15 cells high at median sinus, the disc margins on each side with 1–2 cilia.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5–530 m).

Plants occur in protected, non-exposed sites, such as under cover of *Leptospermum scoparium* in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs, and dwarf heaths to 0.5 m tall, with vegetation dominated by stunted *L. scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus* (at type locality). Also under an open canopy of stunted *Dacrydium cupressinum* and dense *Dracophyllum* understory (ca. 2–3 m above river behind Belltopper Falls). The species also occurs in mosaic communities of stagnant ponds, *Sphagnum* bog, open *L. scoparium – Dracophyllum* heath to 1–2 m tall, and dense communities of *Gleichenia dicarpa* and *E. minus* (Freshwater Landing). At Pryse Peak *Lepidozia serrulata* occurs in open forest, including stunted *Dacrydium cupressinum*, *Podocarpus hallii*, *Olearia colensoi*, *Gahnia*, *Blechnum* and bryophyte cushions on the forest floor. The species is a ground-dweller, occurring on the floor, either over soil or over a layer of thick humus, and at times may form soft cushions.

Comments: *Lepidozia serrulata* is one of only four New Zealand members of the genus with regularly and consistently bipinnate branching (Fig. 45: 1), the others being *L. spinosissima*, *L. microphylla* and *L. pendulina*. The last three species are all erect plants with rigid, woody stems with slender and drooping branches and have leaves that are transversely inserted, typically distant and vertically oriented. *Lepidozia spinosissima*, *L. microphylla* and *L. pendulina* are segregated into three different subgenera in Schuster (2000a) and Engel and Schuster (2001), i.e., *Dendrolepidozia*, *Mastigolepidozia* and *Notholepidozia* respectively. *Lepidozia serrulata* belongs to subgenus *Notholepidozia* and is related to the more specialized taxa in the subgenus, i.e., with *L. kirkii* and *L. hirta* of the same section, sect. *Kirkii*. It differs from *L. kirkii* and *L. hirta* in having the dorsal pair of lobes terminating in a uniseriate row of 4–7 cells, the cells at least at times moderately elongated (2.3–4.3[5.3]:1) (Fig. 45: 12, 13).

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margin). 10, 11. First branch underleaves. 12, 13. Second dorsal-most (left) and dorsal-most (right) leaf lobes (DS = dorsal sinus); both drawn to same scale. 14, 15. Portion of dorsal margin of 2 leaves; both drawn to same scale. 16. Median lobe of underleaf (arrows indicate sinus bases). 17. Stem, cross section. (All from type.)

Sect. ***Austrolepidozia*** R.M.Schust.

Lepidozia sect. *Austrolepidozia* R.M.Schust., Beih. Nova Hedwigia 118: 197. 2000. *Lepidozia* subg. *Austrolepidozia* (R.M.Schust.) R.M.Schust. *in* J.J.Engel & R.M.Schust, Fieldiana, Bot. N.S. 42: 87. 2001. Type: *Lepidozia ulothrix* (Schwägr.) Lindenb.

Lepidozia III. *Incisae* Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 210. 1845, *syn. fide* Engel and Schuster (2001). Lectotype (*fide* Engel and Schuster, 2001): *Lepidozia ulothrix* (Schwägr.) Lindenb.

Lepidozia ulothrix (Schwägr.) Lindenb.

[Fig. 46; Fig. 50: 3, 4, oil-bodies, p. 268]

Jungermannia ulothrix Schwägr., Hist. Musc. Hepat. Prodr. 21. 1814. *Lepidozia ulothrix* (Schwägr.) Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 210. 1845. *Mastigophora ulothrix* (Schwägr.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. Type: "N. Hollandia," without specific locality, "Herb. Ldbg.," *sin. coll.* (G!).

Jungermannia albula Hook.f. & Taylor, London J. Bot. 3: 387. 1844, *syn. fide* Engel and Schuster (2001). *Lepidozia albula* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 211. 1845. *Mastigophora albula* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. Type: Auckland Is., "on *Gottschea lehmanniana*," Nov. 1840, *Hooker* (FH!).

Plants rather delicate, flexuous, with weakly ventrally secund branches, pale olive-green to whitish green, the shoots medium-sized, to 2 cm wide, including branches. Branching exclusively of *Frullania* type, distantly markedly and regularly pinnate, the primary branches short, somewhat curved or hooked at the tip, occasionally becoming flagelliform but not extensively so; secondary branches only sporadically present; branch half-leaf asymmetric to ± symmetric, ovate, 2-lobed, regularly ciliate nearly to the base; first branch underleaf (2)3–4-lobed, inserted on ventral-lateral side of branch and aligned with underleaves of branch. Ventral-intercalary branching lacking. Stems rather soft and flexuous, the cortical cells in 1 layer of weakly to clearly thick-walled cells that are slightly to conspicuously larger than medullary cells; medullary cells distinctly thick-walled. Leaves rigid, strongly concave, with incurved lobes lending the leaves a ± cup-like aspect, imbricate and nearly or completely hiding stem in dorsal view, 0.4–1.2 mm long at longest point, 0.7–2.2 mm wide at widest point, patent, the insertion distinctly incubous and slightly recurved at dorsal end; leaves distinctly asymmetric, unequally 4-lobed, the leaves divided to ca. 0.4–0.65 (median sinus), the distance from dorsal sinus base to insertion much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes of differing shape, the dorsal pair of lobes caudate, the ventral lobe linear to attenuate, the lobes with 1 to (less often) several pairs of opposing spines (1[2], non-opposing spines per lobe in suboptimal plants), the dorsal lobes 7–10 to 13–15 cells wide at base, the ventral lobe 6–9 cells wide at base, the lobes terminating in a uniseriate row of 5–7 to 8–10(15) cells (the ventral typically the longest); cells of uniseriate row capillary, elongated (3–4:1), thick-walled and with the septa thickened and swollen. Disc distinctly asymmetric primarily due to strong dilation of dorsal sector, the dilated portion up to a third of the disc area, the disc 18–26 cells high at dorsal sinus, 6–13 cells high at ventral sinus; dorsal margin and the confluent margin of the dorsal lobe with 7–8 to 12–19 spinose teeth or cilia that terminate in a uniseriate row of 2–5(6) cells; ventral margin entire or sporadically with 1–2 well-developed spines or laciniae. Cells of disc-middle evenly thick-walled,

elongate, 12–20 μm wide × 24–42 μm long; cells in the ampliate sector and median lobe cells shorter, 14–18 μm wide × (17)20–26 μm long; median basal cells enlarged and in a rather distinct field; surface smooth to finely striate-papillose. Oil-bodies occupying small portion of cell lumen, hyaline and glistening, 2–5(6) per cell, subglobose to elliptic to fusiform, coarsely papillose or finely botryoidal, the spherules soon coalescing and the oil-bodies soon very coarsely botryoidal, the oil-bodies mostly 4–6 μm in greater diam., fleeting; basal cells with (3)4–6 per cell, spherical and 3–5 μm in diam., or citron-shaped and 3 × 4.5 μm. Underleaves 1.5–2× stem width, spreading, symmetrically basically 4-fid to ca. 0.45–0.65 (median sinus), the sinus bases plane, the lobes distinctly broadly incurved, the lobe base ± parallel sided, 8–9 cells wide, the summit of median lobes truncate and ± regularly ciliiform and 2–3-fid, the distal sector setaceous, terminating in a uniseriate row of 5–8 to 8–13 cells; disc 10–13 cells high at median sinus, the disc margins on each side with 1–2 cilia.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, cernuous ventral-intercalary branches from main shoot and primary and secondary branches; bracts ventricose-cucullate, 2-lobed to ca. 0.4, the lobes acuminate, terminating in a uniseriate row of 2–4 elongated cells, the lobe margins with several spinose teeth; antheridial stalk biseriate. Gynoecia not seen.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island, South Island ([330]600–1200 m), North Island (ca. 900 m); Australia: Tasmania, southeast Australia. In New Zealand known from Fiordland, Westland, Canterbury (Arthur's Pass), Western Nelson and Southern North Island (Tararua Ra.) EPs.

Known from Stewart Island and scattered sites in the southern half of the South Island, plus a single North Island site. In the Haast River area (sea level) the species occurs in mucky niches at the sides of mounds in open swampy areas with *Sphagnum* and scattered *Leptospermum scoparium* and others. It is also present at a low-altitude site in the Cascade ultramafic moraine (Cascade Road, South Westland, ca. 35–135 m), an area characterized by ultramafic rocks and outcrops with rather open vegetation consisting mainly of *Gleichenia*, *Lycopodium*, *Juncus*, the lichen *Cladonia* and scattered *Leptospermum scoparium*; at this site the species is terricolous among *Restionaceae*. Also known at higher altitude from Bealey Glacier Track (Arthur's Pass Natl. Park, 915 m), at the bottom of an earth hummock, forming loose wefts over duff in a *Nothofagus solandri – Coprosma pseudocuneata – Dracophyllum longifolium – Phyllocladus alpinus* forest on a flat river terrace. On the Auckland Islands, it is common in *Metrosideros umbellata – Myrsine divaricata – Dracophyllum longifolium* forest, but also in open sites of *Chionochloa antarctica* tussockland and *Oreobolus pectinatus* moorlands.

In upper montane forest and scrub of *Dacrydium cupressinum*, *Nothofagus solandri*, *N. fusca*, *Metrosideros umbellata*, *Halocarpus biformis*, *Lepidothamnus intermedius*, *Archeria traversii* and *Olearia colensoi*, where it may become locally common. Accompanying species are *Acromastigum anisostomum*, *Anastrophyllum schismoides*, *Bazzania novae-zelandiae*, *Breutelia pendula*, *Dicranoloma robustum*, *Heteroscyphus billardierei*, *H. decipiens*, *Hymenophyllum multifidum*, *Jamesoniella colorata*, *Lepicolea attenuata*, *Lepidogyna hodgsoniae*, *Luzuriaga parviflora*, *Marsupidium surculosum*, *Megalembidium insulanum*, *Ptychomnion aciculare*, *Rhacocarpus purpurascens*, *Rhaphidorrhynchium amoenum*, *Riccardia cochleata*, *R. crassa*, *Saccogynidium australe*, *Schistochila balfouriana*, *Treubia lacunosa*, *T. pygmaea*, *Trichotemnoma corrugatum* and *Verdoornia succulenta*.

Comments: *Lepidozia ulothrix* is a robust plant, with 1-pinnate branching, the branches distant, abbreviated and somewhat curved. The leaf armature of *L. ulothrix* is more copious than

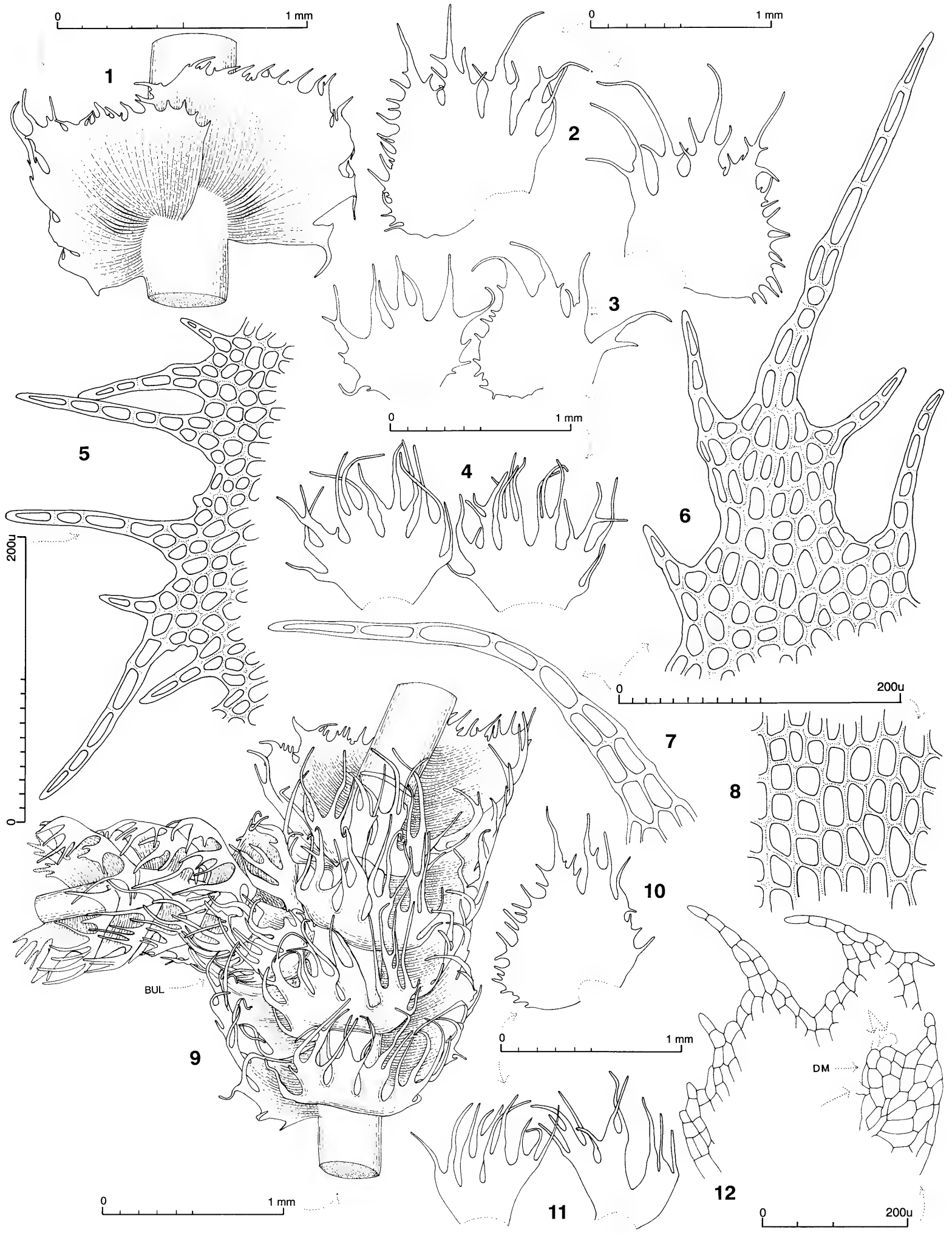

Fig. 46.
Lepidozia ulothrix (Schwägr.) Lindenb. 1. Sector of main shoot, dorsal view. 2. Leaves. 3. Underleaf and to right, leaf. 4. Underleaves. 5. Sector of dorsal margin of leaf. 6. Portion of dorsal lobe. 7. Distal sector of dorsal-most leaf lobe. 8. Median disc cells of leaf. 9. Sector of main shoot with *Frullania*-type branch, ventral view (BUL = first branch underleaf). 10. Half-leaf. 11. First branch underleaves. 12. ♂ Bract (DM = dilated dorsal margin, slime papillae at arrows). (Figs. 1, 2, 4–6,

in *L. hirta*, with longer and more numerous spines and/or cilia on the dorsal margin and confluent margin of the dorsal lobe. The lobe margins are armed with several, often opposing spines, and the cells of the uniseriate row are more elongated.

Subg. ***Glaucolepidozia*** R.M.Schust.

Lepidozia subg. *Glaucolepidozia* R.M.Schust., J. Hattori Bot. Lab. 36: 386. 1973 (1972). Type: *Lepidozia glaucophylla* Steph.
Lepidoziopsis E.A.Hodgs., Rec. Domin. Mus. 4: 105. 1962.

Lepidozia glaucophylla (Hook.f. & Taylor) Gottsche, Lindenb. & Nees

[Fig. 47]

Jungermannia glaucophylla Hook.f. & Taylor, London J. Bot. 3: 580. 1844. *Lepidozia glaucophylla* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 207. 1845. *Mastigophora glaucophylla* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Lepidoziopsis glaucophylla* (Hook.f. & Taylor) E.A.Hodgs., Rec. Domin. Mus. 4: 106. 1962. Lectotype (*fide* Engel and Schuster, 2001): Tasmania, 1840, *Hooker* (FH!).

Plants prostrate, in loosely interwoven pure mats or as conspicuous, isolated strands growing among other matted bryophytes, slender, with spreading branches, glaucous, whitish to ceraceous, the older sectors subnitid and brownish (as if scorched), the surface dull, waxy and water-repellent, the shoots medium, to 1.5 cm wide, including branches. Branching mostly of *Frullania* type, ± distantly 1(2)-pinnate, the branches gradually tapering, occasionally whip-like, flagelliform and microphyllous; secondary branches occasional on well-developed shoots; branch half-leaf broadly ovate, slightly asymmetrical, cordate at base, 2-lobed to ca. 0.2–0.3, the margin sinuate, or bluntly toothed; first branch underleaf large, mostly undivided, occasionally 2- or 3-lobed, inserted on ventral-lateral side of branch at or near junction of branch and main shoot, aligned with underleaves of branch. Ventral-intercalary branches sporadically produced. Stem epidermal cells in surface view ± thick-walled, with a waxy coating like that of the leaves, the cortex in 1 layer of thin to slightly thick-walled cells ± distinctly larger than the medullary cells; medullary cells slightly thickened. Leaves involute and subamplexicaul when dry, when moist spreading and divergent, rather strongly concave, contiguous to imbricate, at times nearly or completely hiding stem in dorsal view, uniform in size (not in sequential sectors of varying size), 0.6–0.7 mm long and wide, the insertion broad, moderately to strongly incubous; leaves asymmetric, ± equally 4-lobed, the leaves divided to ca. 0.4–0.5 (median sinus), the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes subcaudate, entire, abruptly narrowing to a uniseriate row of 3–5(6) cells; cells of uniseriate row and often the subtending lobe cells elongated (to 2:1), thick-walled, the terminal cell tapering to a point; dorsal lobe 5–7 cells wide at base. Disc distinctly asymmetric due to ampliation of dorsal margin, the dorsal sector to one third the disc area, 14–18 cells high at dorsal

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8–11, from *Fife 8987*, New Zealand, South Is., Arthur's Pass Natl. Park, Bealey Glacier Track; 3, 7, from type of *L. albula*.)

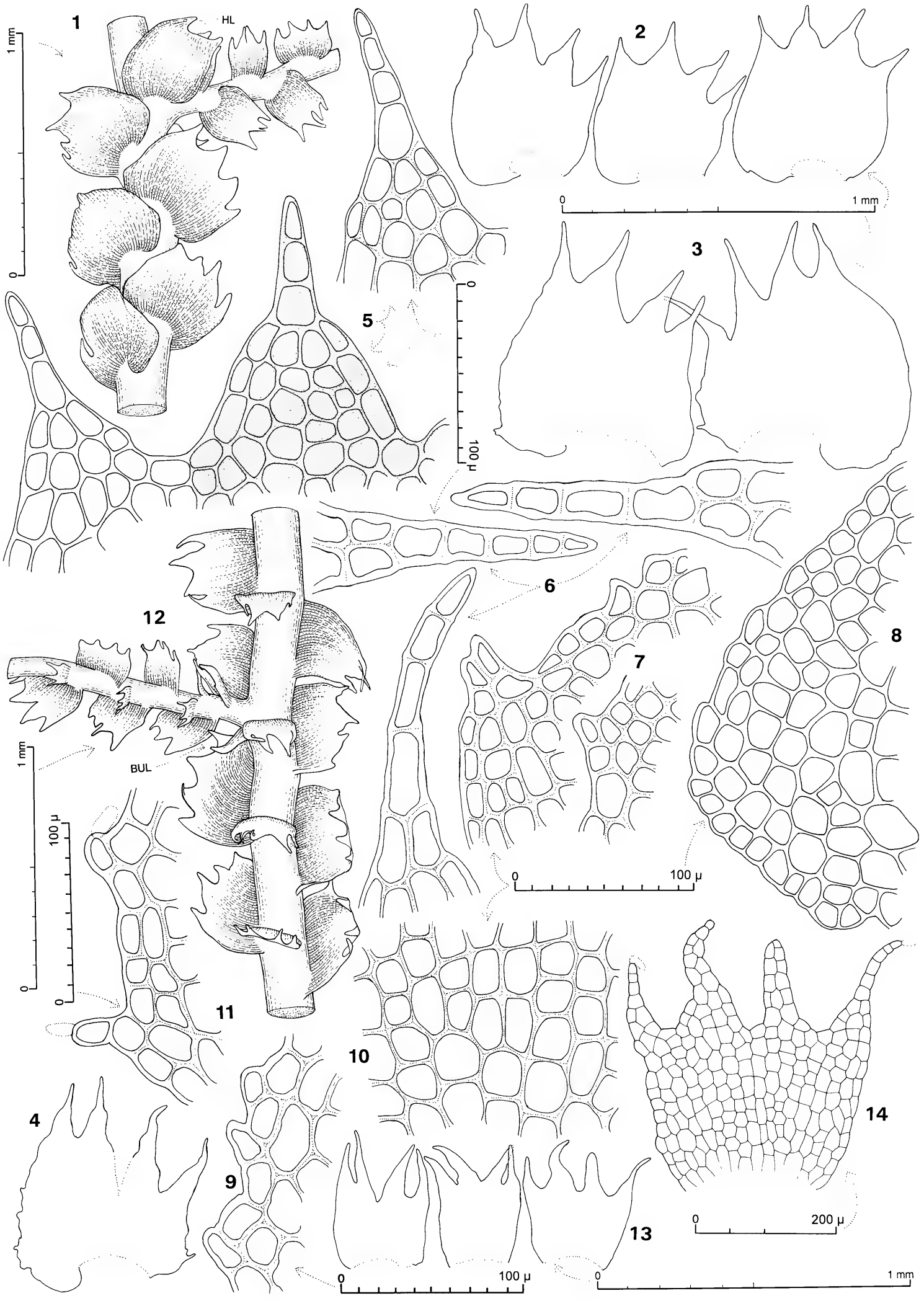

Fig. 47.
Lepidozia glaucophylla (Hook.f. & Taylor) Gottsche, Lindenb. & Nees. 1. Sector of main shoot, dorsal view (HL = half-leaf). 2–4. Leaves (all at same scale). 5. Dorsal-most lobe (above) and dorsal pair of lobes, the surface detail shown for lobe at right. 6. Median lobes of leaves (all at same scale). 7–9. Marginal cells of ampliate sector (dorsal, basal portion) of leaf disc. 10. Median disc

sinus, 10–14 cells high at ventral sinus, the dorsal margin subentire to sinuate to distantly and irregularly armed with 1–2-celled teeth, the margin auriculate at the base, the ventral subcordate at the base, occasionally with a small tooth or short spine. Cells of disc and lobes rounded quadrate, evenly thick-walled, trigones absent, the median disc cells 20–26 × 22–30 μm; marginal cells of disc and lobes typically with a thickened outer wall; surface a dense and coarsely granular coating. Underleaves inserted on 8–9 rows of stem cells, distinctly spreading, ca. 1–1.3× stem width, symmetrically 4-fid to ca. 0.4 (median sinus), the lobes plane, narrowly attenuate and consisting of several tiers of 2 laterally juxtaposed cells and then rounded at the tip, or, more commonly, terminating in a uniseriate row of 2–4 cells; disc 9–12 cells high at median sinus, the margins plane, occasionally with a 1–2-celled tooth that terminates in a slime papilla.

Androecia and gynoecia not seen.

Distribution and Ecology: New Zealand: South Island (695–1200 m); Australia: Tasmania, Victoria, New South Wales. Apparently very rare in New Zealand and known only from a few South Island sites. Known from four Fiordland sites: at 695 m at Lake Marion in a rather open *Nothofagus menziesii* forest, with frequent large boulders that are often largely bryophyte covered. At this site, plants of *Lepidozia glaucophylla* together with hymenophylls formed a thick mass that was loosely attached to a huge boulder (see Engel and Schuster, 2001). Known from Mackinnon Pass at 1000 m on a rock overhang; from the Borland Burn (also Fiordland) in bryophyte cushions under *N. solandri* var. *cliffortioides* forest, and from Deep Cove. Also known from two sites on the Paparoa Ra. (Mt. Euclid and Mt. Priestly, 960–1200 m) on humus over rock in *N. menziesii* forest with abundant *Dracophyllum traversii*, and from a rock overhang in *Chionochloa australis* grasslands. Accompanying species are *Bazzania nitida*, *Dicranoloma dicarpum*, *Distichophyllum pulchellum*, *Lepidozia kirkii*, *Leptotheca gaudichaudii*, *Mittenia plumula*, *Plagiochila retrospectans*, *Pyrrhobryum mnioides*, *Rhizogonium distichum* and *Weymouthia cochlearifolia*.

Comments: *Lepidozia* species with a waxy, water-repellent "bloom" on the surface of the stems and leaves had been understood as constituting a single species, *L. glaucophylla*. In fact, however, in New Zealand four distinct elements are represented: *L. glaucophylla s. str.*, *L. bisbifida* Steph., *L. digitata* Herzog and *L. glaucescens* J.J.Engel.

Lepidozia glaucophylla is similar to *L. bisbifida* in the conspicuous water-repellent "bloom" on the surface of the stem and leaves, and the strongly incubous, subsymmetrically lobed leaves (Fig. 47: 1–3). It is immediately distinguishable, however, by the broadly ampliate and strongly auriculate dorsal margin of the leaf (Fig. 47: 1–4, 8); the irregularly sinuate to toothed leaf margins (Fig. 47: 7–9); the evenly thick-walled disc cells (Fig. 47: 7, 9, 10); the subcaudate, abruptly tapering leaf lobes, which terminate in a uniseriate row of 3–5 elongated cells (Fig. 47: 4–6); and the oblique to longitudinal insertion of the first branch underleaf at the base of the branch, rather than transversely inserted on the ventral-lateral face of the stem, as in *L. bisbifida*.

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cells. 11. Portion of ventral margin of leaf disc. 12. Sector of main shoot with *Frullania*-type branch, ventral view (note first branch underleaf = BUL). 13. Underleaves. 14. Underleaf, cellular detail. (Figs. 1, 2, 5, 8, 10, 12–14, from type; 3, 7, 11, from *Fife 6442*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., Mt. Euclid; 4, 6, 9, from *Engel 23170*, New Zealand, South Is., Fiordland EP, Fiordland Natl. Park, S end of Lake Marion.)

Lepidozia bisbifida Steph.

Lepidozia bisbifida Steph., Sp. Hepat. 3: 593. 1909. Type: New Zealand, without specific locality, *Kirk s.n.* (G!).

Lepidozia subquadrata Steph., Sp. Hepat. 6: 341. 1922. Type: New Zealand, "alpine interior," without specific locality, *Colenso* "*inter 2064*" (G!).

Lepidozia brevipinna Pearson, Univ. Calif. Publ. Bot. 10: 321. *pl. 94*. 1923. Type: New Zealand, North Is., Wairakei, Waiora Valley, 4 May 1904, *Setchell 9* (UC!).

Plants prostrate to loosely procumbent, the stems loosely interwoven, flexuous, with spreading branches, glaucous and ash grey to ivory, the older shoot sectors burnt orange or lightly tinged with brown as if scorched, the surface dull and water-repellent; shoots medium-sized, to 1.5 cm wide, including branches (sporadically large and to 2 cm wide [including branches] × 7.5 cm long). Branching nearly exclusively of *Frullania* type, rather short, closely and regularly 1-pinnate to locally 2-pinnate, the branches abruptly tapering, occasionally becoming ± whip-like, flagelliform and microphyllous; secondary branches occasional; branch half-leaf broadly ovate, subsymmetrical, subcordate at the base, 2-lobed to ca. 0.2–0.3, the dorsal lobe often smaller; first branch underleaf large, often squarrose-reflexed, 2–4-lobed (rarely undivided), usually on lateral or ventral-lateral side of stem, often somewhat below the branch, aligned with leaves of main shoot or underleaves of branch. Ventral-intercalary branching occasional, leafy. Stem epidermal cells thin-walled, with a waxy coating like the cells of the leaves. Leaves involute-triangular and distinctly amplexicaul when dry, when moist rigid, distinctly concave to nearly cup-like, approximate to contiguous, intermittently large and small along length of stem, those in well-developed sectors 0.8–1.3 mm long and wide, the leaves of smaller sectors as small as 0.5 mm long and wide, the leaves spreading, nearly horizontal, the insertion broad, strongly incubous; leaves subsymmetric to moderately asymmetric, typically ± equally 4-lobed (rarely bisbifid), the lobes sometimes in turn divided, the leaves then appearing 5–8-lobed, the leaves divided to ca. 0.2–0.5 (median sinus), the distance from dorsal sinus base to insertion subequal to or not much greater than that from ventral sinus to insertion, the sinuses of subequal depth or gradually becoming deeper ventrally. Lobes acute to apiculate, terminating in a single cell or more commonly a uniseriate row of 2–3 cells; cells of uniseriate row ± isodiametric or slightly longer than wide, thin-walled, the terminal cell strongly tapering; median pair of lobes somewhat larger, 6–8(11) cells wide at base, the dorsal lobes (2)3–5 cells wide at base. Disc subsymmetric, (13)15–22(28) cells high at dorsal sinus, 9–14 cells high at ventral sinus, the margins usually entire, the dorsal margin moderately ampliate, sporadically with 1 or more blunt teeth or sinuate, cordate at the base, the ventral margin occasionally with a slender lobuliform process. Cells of disc and lobes uniformly thin-walled, with conspicuous intercellular pits, trigones minute to medium, the median disc cells (18)24–40 × 28–40 μm; median basal cells not differentiated; marginal cells of disc smaller, those of disc and lobes sporadically with thickened outer walls, but rarely consistently so; surface a dense granular coating that ultimately develops cracks or fine fissures (especially over the vertical cell walls), the cell outlines obscured by the scurfy, water-repellent coating. Oil-bodies absent in many leaf cells, otherwise (1)2–3 per cell, colorless, coarsely to moderately botryoidal, spherical and ca. 3 μm in diam. or ellipsoidal with acute tips and 2–3 × 4.5–8 μm, as large as 4 × 10 μm at leaf base, fleeting. Oil-bodies (Engel and Schuster, 2001) small and inconspicuous, 2–5 to (0)4–6(9) per cell, few (often only 3–6[9]) segmented, coarsely botryoidal, much smaller than chloroplasts, often 3 × 6 μm and consisting of a large

spherule at each end and 4–6 smaller ones centrally. Underleaves inserted on 9–10 rows of stem cells, widely spreading, ca. 0.7–1× stem width, asymmetrically or symmetrically 4-fid to ca. 0.3–0.45 (median sinus), the underleaves often with 1, 2 or all 3 sinuses narrow, slit-like and the lobes adnate by the surface covering, the underleaves then *in situ* appearing 2- or 3-lobed, the lobes plane, attenuate to acuminate, consisting of several tiers of 2 laterally juxtaposed cells and then rounded at the tip, or, more commonly, terminating in a single cell or a uniseriate row of 2–4 cells that often terminate in a slime papillae; disc 5–9 cells high at median sinus, the margins plane, entire.

Plants dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, often cernuous ventral-intercalary branches from main shoot; bracts ventricose-cucullate, 2-lobed to ca. 0.3, the lobes acute to short-acuminate; antheridial stalk biseriate. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Antipodes Islands (150 m), South Island (200–1350 m), North Island (300–500 m). Known from Fiordland, Southland (Ajax Hill), Otago, Westland, Canterbury (Arthur's Pass, Woolshed Hill), Western Nelson (Paparoa Ra.) and Volcanic Plateau (Tokaanu, Rotorua) EPs.

A species occurring mainly in forests of *Nothofagus solandri* and *N. menziesii* ranging from as low as 200 m, but, more often, from over 750 m to treeline. Also known from *Metrosideros umbellata – Podocarpus hallii – Dracophyllum traversii* upper montane forest. It is found on rotted wood (particularly where there is cover of other bryophytes, along with, at times, hymenophylls) or deep in shaded, moist, sheltered pockets of tree bases, boulders or rotted logs. Also on shaded cliff bases, particularly where soil has accumulated, and plants are notable as scattered glaucous patches among other bryophytes. It often grows loosely attached and may be locally very common. The species at times covers large areas, but typically does not become matted or pure. However, pure mats are at times formed deep in sheltered recesses. Accompanying species in forest habitats are *Adelanthus falcatus*, *Bazzania adnexa*, *B. nitida*, *Categonium nitens*, *Chandonanthus squarrosus*, *Chiloscyphus leucophyllus*, *Dicranoloma robustum*, *Distichophyllum pulchellum*, *Hymenophyllum multifidum*, *Hypnum chrysogaster*, *Lepidozia pendulina*, *Rhizogonium distichum*, *Weymouthia cochlearifolia* and *Zoopsis argentea*. In the penalpine zone over soil deep in protected recesses between boulders or under boulder overhangs, as well as on the sides of rills. In the alpine zone on shaded, damp slopes under cover of *Chionochloa* tussocks. Also known from the geothermal areas of the North Island (see Engel and Schuster, 2001) where it is found on sinter, often under *Leptospermum scoparium*, *Kunzea ericoides* and *Cyathodes fasciculata* scrub with *Campylopus capillaceus*. On the Antipodes Islands, it occurs in *Chionochloa antarctica* tussocklands with *Campylopus introflexus*, *Lepidogyna hodgsoniae* and *Leptotheca gaudichaudii*.

Comments: This is the species long known in the New Zealand literature as *Lepidozia glaucophylla*. *Lepidozia bisbifida* is readily distinguished from *L. glaucophylla* by the broadly inserted, deeply concave, involute leaves; by the leptodermous leaf cells with small to minute trigones; and by the ± transverse insertion of the first branch underleaf on the stem, often some distance below the associated branch. Another feature of this species is the intermittently large and small leaf size along the length of the stem. (See also comments under *L. glaucophylla*.)

The species is quite distinct in the field due to the large plant size coupled with the glaucous condition, with older portions of the plants often burnt orange or lightly tinged with brown and then appearing as if scorched.

Lepidozia digitata Herzog

[Plate 5A, B; Fig. 48; Fig. 50: 2, oil-bodies, p. 268]

Lepidozia digitata Herzog, Trans. & Proc. Roy. Soc. New Zealand 68: 45. *pl. 5*, *m–n*. 1938. Holotype: New Zealand, near Atiamuri, *Allison 72* (JE!).

Plants prostrate, the stems loosely interwoven, flexuous, with widely spreading branches, glaucous to ivory, the older shoot sectors tinged with brown, the surface dull and water-repellent; shoots small, to 0.6 cm wide, including branches. Branching exclusively of *Frullania* type, the

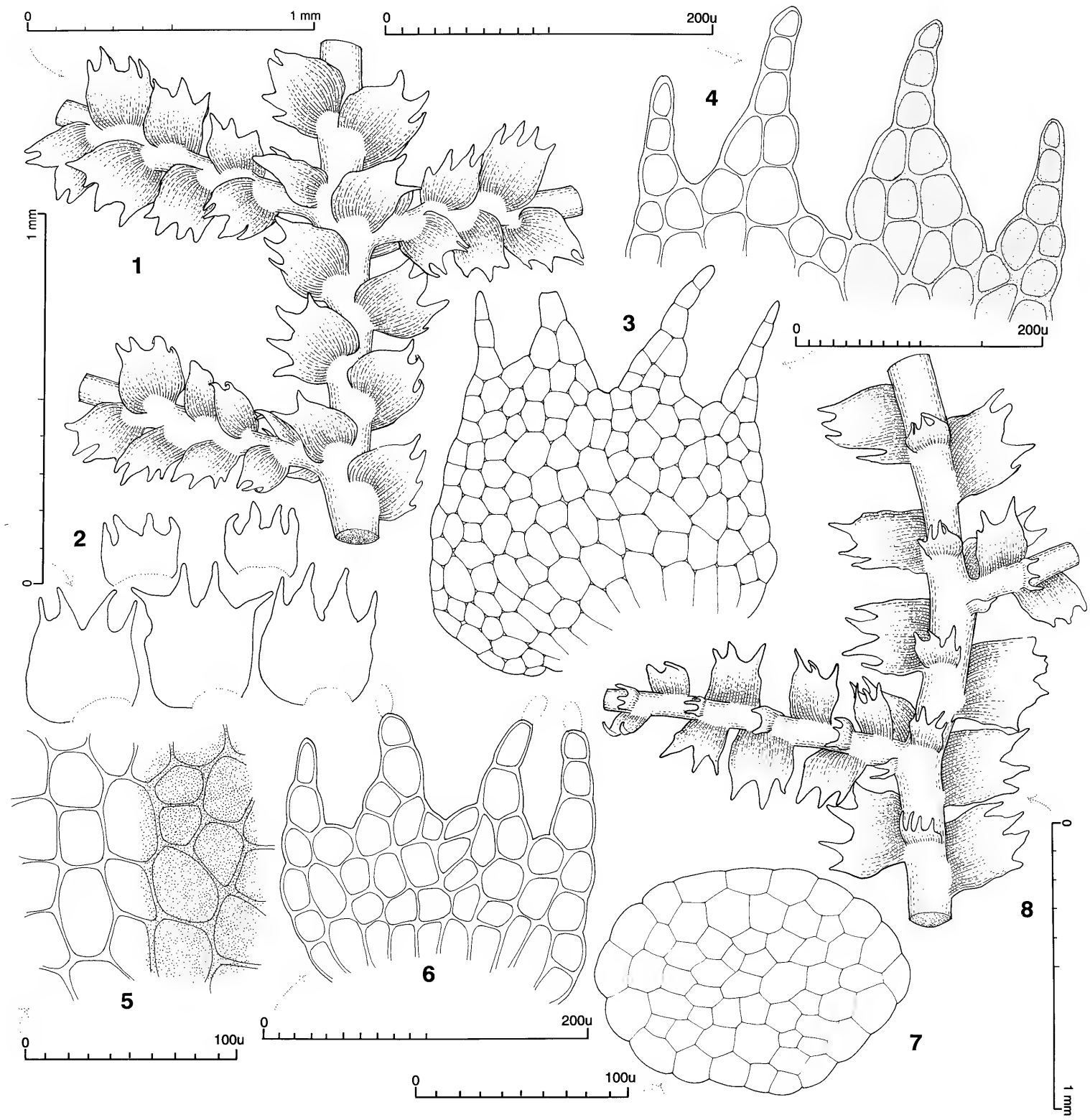

Fig. 48.
Lepidozia digitata Herzog. 1. Sector of main shoot, dorsal view. 2. Leaves and above, underleaves. 3. Leaf, cellular detail. 4. Leaf lobes, surface detail indicated in part. 5. Median disc cells, surface detail indicated in part. 6. Underleaf, cellular detail. 7. Stem, cross section. 8. Sector of main shoot with 2 *Frullania*-type branches, ventral view (note undivided and, lower, bilobed first branch underleaves, the latter is the typical condition). (All from type.)

branches rather short, rather distant and irregularly pinnate, the branches short and not tapering or only sporadically becoming flagelliform and microphyllous; branch half-leaf narrowly ovate, subsymmetrical, subcordate at the base, 2-lobed to ca. 0.2–0.3; first branch underleaf 2-lobed (occasionally undivided), inserted on ventral-lateral side of main shoot at branch base and obliquely to subvertically inserted. Ventral-intercalary branching not seen. Stem epidermal cells thin-walled, with a waxy coating like the cells of the leaves, the cortex in a single row of cells that are slightly smaller to or at most feebly larger than those of the medulla. Leaves with margins somewhat involute when dry, when moist plane to slightly concave, distant to contiguous, ± uniform in size, 0.35–0.55 mm wide × 0.4–0.55 mm long, spreading, nearly horizontal, the insertion broad, strongly incubous; leaves at most moderately asymmetric, (3)4-lobed to ca. 0.35 (median sinus), the distance from dorsal sinus base to insertion not much greater than that from ventral sinus to insertion, the sinuses gradually becoming deeper ventrally. Lobes subacuminate, terminating in a uniseriate row of 2–3(5) cells; cells of uniseriate row ± isodiametric or somewhat longer than wide, thin-walled, the terminal cell tapering to a rounded apex; median pair of lobes somewhat larger, 3–5(6) cells wide at base, the dorsal lobe 2–3(4) cells wide at base. Disc subsymmetric, (6)7–13(16) cells high at dorsal sinus, 6–13 cells high at ventral sinus; dorsal margin scarcely ampliate, entire or somewhat sinuate, sporadically with a 1-celled tooth, feebly cordate at the base; ventral margin entire. Cells of disc and lobes uniformly thin-walled, trigones none or minute, the median disc cells 24–35 μm wide × 29–42 μm long; median basal cells somewhat elongated but otherwise not differentiated; marginal cells of disc (especially the dorsal) often with a somewhat thickened, concave outer wall (the wall thickening somewhat crescentic and bulging into the cell lumen); surface finely granular, the cell outlines obscured by the scurfy, water-repellent coating. Oil-bodies fleeting, occupying very small portion of cell lumen, hyaline, 4–6 per disc cell, sometimes absent from most cells, finely botryoidal, rather quickly breaking up by coalescing of spherules, many oil-bodies spherical and 2.5–5 μm in diam. or ellipsoidal with acute tips and 2–2.5 × 3–6 μm, in basal cells also often absent or 1–3 per cell and larger, spherical, 4.5–5.5 μm in diam. Chloroplasts large for cell size, about the same size as oil-bodies. Underleaves inserted on 3–4 rows of stem cells, small, slightly spreading, ca. 1–1.3× stem width, ± symmetrically 3–4-fid to ca. 0.5–65 (median sinus), the sinuses broad to narrow, the lobes slender, 2–3(4) cells wide at the base and often uniseriate for most of their length, the uniseriate row of 2–3 cells and often terminating in a slime papilla; disc (1.5)2–4 cells high at median sinus, the margins plane, entire. Asexual reproduction sporadically present, via fragmenting or caducous leaf lobes, whose bases persist as truncate stubs.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (480–1390 m), North Island (660–1220 m). Known from Fiordland, Otago (Rees Valley), Westland (Nelson Lakes Natl. Park), Canterbury (upper Rakaia and Waimakariri valleys), Volcanic Plateau (Mt. Ruapehu), Taranaki, Gisborne and Auckland EPs.

The few, scattered stations for the species are for the most part within *Nothofagus solandri* var. *cliffortioides*, *N. fusca* and *N. menziesii* forests ranging from 630 to 1390 m. Also known from *Weinmannia racemosa – Metrosideros umbellata* forest. It occurs in shaded, protected, often deep pockets (such as the hollowed recesses of tree bases), or in crevices and recesses of outcrops, or over soil of steep, mossy banks, where it may occur, for example, in a protected niche under the lip of the forest edge at the upper extremity of a stream bank (Lakehead Track, Nelson Lakes Natl. Park). Also known from below the summit of "Little Moehau" (Coromandel Forest Park, ca. 800 m) in a mosaic of *Sphagnum* bog and small communities of shrub-heath including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus*

pectinatus, *Corokia buddleoides* and occasional stunted *Weinmannia silvicola* and *Dacrydium cupressinum*. At this site plants occurred very loosely creeping over soil in a shaded niche in a thicket. Also in *Podocarpus nivalis – Chionochloa pallens* shrubland. Accompanying species are *Balantiopsis diplophylla*, *Bazzania nitida*, *Categonium nitens*, *Ditrichum*, *Leptophyllopsis laxus*, *Leptotheca gaudichaudii*, *Ptychomnion aciculare*, *Rhizogonium distichum* and *R. pennatum*.

Rarely seen as an epiphyte on caudices of *Dicksonia squarrosa* with *Hymenodon pilifer*.

Comments: *Lepidozia digitata* is the smallest of the four New Zealand species of subg. *Glaucolepidozia*, with leaves at most 0.5 mm in longest dimension. Hodgson (1956) treated *L. digitata* as a small-leaved expression of "*L. glaucophylla*" (i.e., *L. bisbifida*), but it differs in being only one third the size. *Lepidozia digitata* is not only the smallest species of *Glaucolepidozia*, it has the most remote leaves (Fig. 48: 1, 8). Notable also is the apparent reproduction via fragmenting leaf lobes, whose bases persist as truncated stubs. The leaf lobes mostly end in 3 superposed cells (Fig. 48: 3, 4) but on weak phases sometimes in 4–5 cells. Stems are weaker in *L. digitata* than in other *Glaucolepidozia* species; on weak phases they may be only 6 cells high, ranging to 8–9 cells high in vigorous phases (Fig. 48: 7).

Lepidozia glaucescens J.J.Engel

[Plate 5C; Fig. 49]

Lepidozia glaucescens J.J.Engel *in* J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 42: 101. *f. 39*. 2001. Holotype: New Zealand, South Is., Nelson/Westland Prov. boundary, Pororari River Track, 5 km from road, ca. 500 ft., *Child H4966* (F); isotype: (CHR).

Plants loosely creeping, or if on vertical banks, then oriented stiffly from substrate, in loosely interwoven mats, the shoots slender, fragile, with widely spreading branches, fragile, brownish and subnitid to glaucous and ivory-white (at least on new growth), the surface then dull and water-repellent, the shoots medium, to 2.5 cm wide, including branches. Branching nearly exclusively of *Frullania* type, ± regularly 1-pinnate to remotely 2-pinnate, the branches gradually tapering, becoming whip-like, flagelliform and microphyllous; secondary branches sporadic; branch half-leaf narrow, linear, subsymmetrical, subcordate at the base, 2-lobed to ca. 0.4; first branch underleaf mostly undivided, less commonly 2(4)-lobed, inserted on ventral-lateral side of branch base and aligned with underleaves of branch. Ventral-intercalary branching rare, leafy. Stem epidermal cells in surface view rather thick-walled, sometimes with a waxy coating like that of the leaves. Leaves fragile, when dry moderately concave, with the lobes curved ventrally; leaves when moist explanate, with spreading lobes, ± distant to contiguous, with much of stem visible in dorsal view, uniform in size (not in sequential sectors of varying size), narrowly inserted and somewhat longer than wide, 0.3–0.5(0.6) mm long and wide, spreading, the insertion varying from weakly to distinctly incubous; leaves moderately to distinctly asymmetric, unequally 4-lobed, the leaves divided to ca. 0.4–0.55 (median sinus). Lobes narrowly attenuate to acuminate, the dorsal lobes ± paired, the ventral shorter than the dorsal lobes and somewhat divergent, the lobes terminating in a uniseriate row of 3–4(5) cells; cells of uniseriate row isodiametric to ± elongated (to 2:1), thick-walled and often with somewhat swollen septa, the terminal cell often moderately to distinctly elongated, tapering to a point; the dorsal lobe 3–4(5) cells wide at base; surface of lobes striate-papillose, the papillae mostly obscured by the thin and continuous granular coating. Disc moderately to distinctly asymmetric, obliquely truncate and deltoid, 8–12 cells high at dorsal sinus, 5–9 cells high at ventral sinus; dorsal margin ± straight, abruptly cordate at the base, entire; ventral margin en-

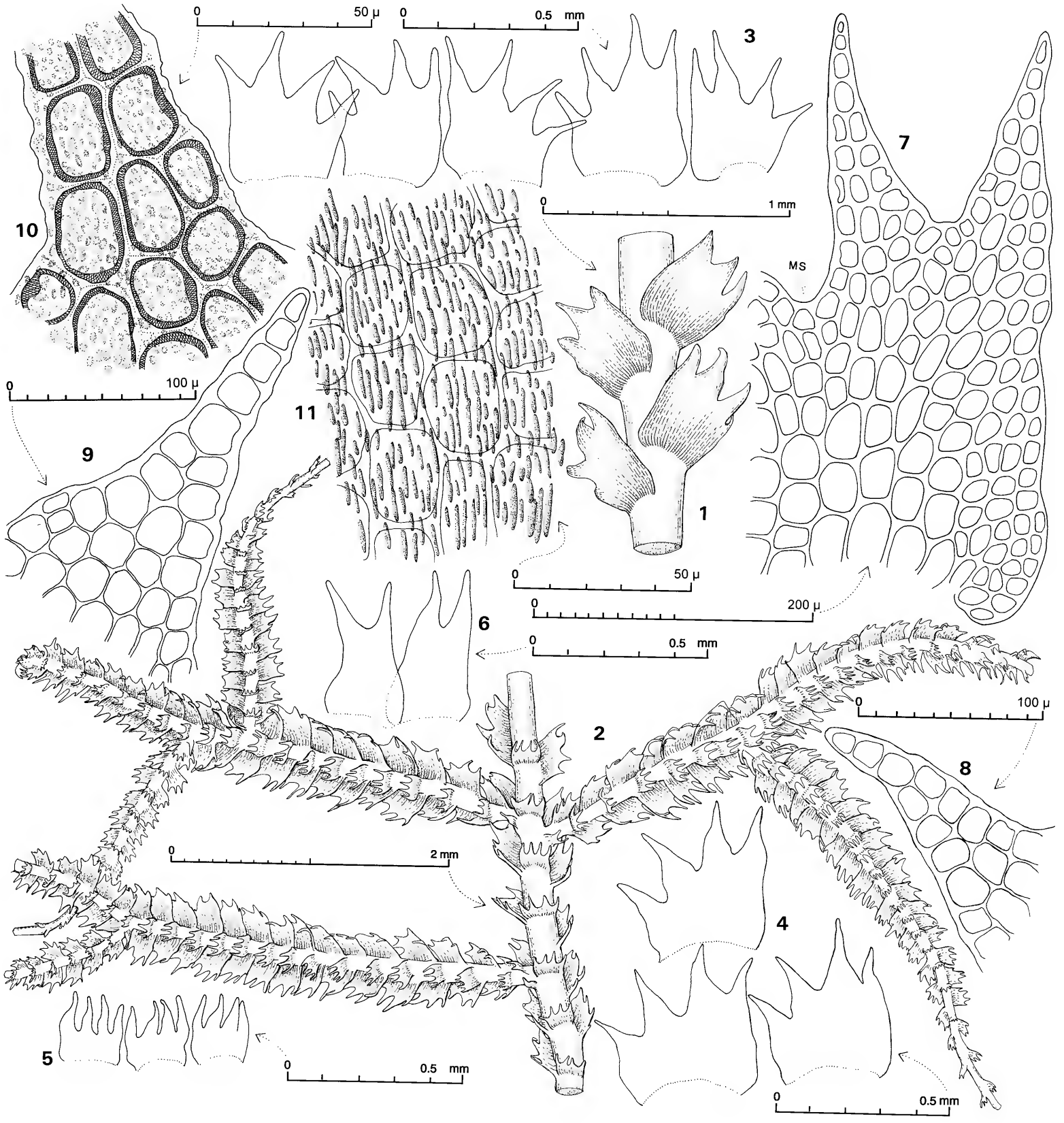

Fig. 49.
Lepidozia glaucescens J.J.Engel. 1. Sector of main shoot, dorsal view. 2. Sector of main shoot, ventral view. 3, 4. Leaves. 5. Underleaves. 6. Half-leaves. 7. Dorsal half of leaf (MS = median sinus). 8. Outer (dorsal-most) lobe of dorsal half of leaf (surface detail not shown). 9. Median lobe of dorsal half of leaf (surface detail not shown). 10. Portion of dorsal lobe showing papillae on surface, granular coating and lamellated cell walls (cross-hatched shading). 11. Median cells of dorsal half of disc showing striate surface. (Figs. 1–3, 5–7, 10, from type; 4, 8, 9, 11, from *Engel 21087*, New Zealand, North Is., Northland EP, SE corner of Waipoua Forest.)

tire. Cells of disc-middle thick-walled, with trigones small, the cells somewhat longitudinally elongated, 18–24(28) µm wide × 21–30 µm long, the cells of the narrow dorsal sector smaller and quadrate; median basal cells in 1 (locally 2) rows of enlarged cells; marginal cells of disc and lobes typically with a thickened outer wall (the wall thickening often crescentic and bulging into the cell lumen); surface of disc as in lobes. Underleaves inserted on 4–6 rows

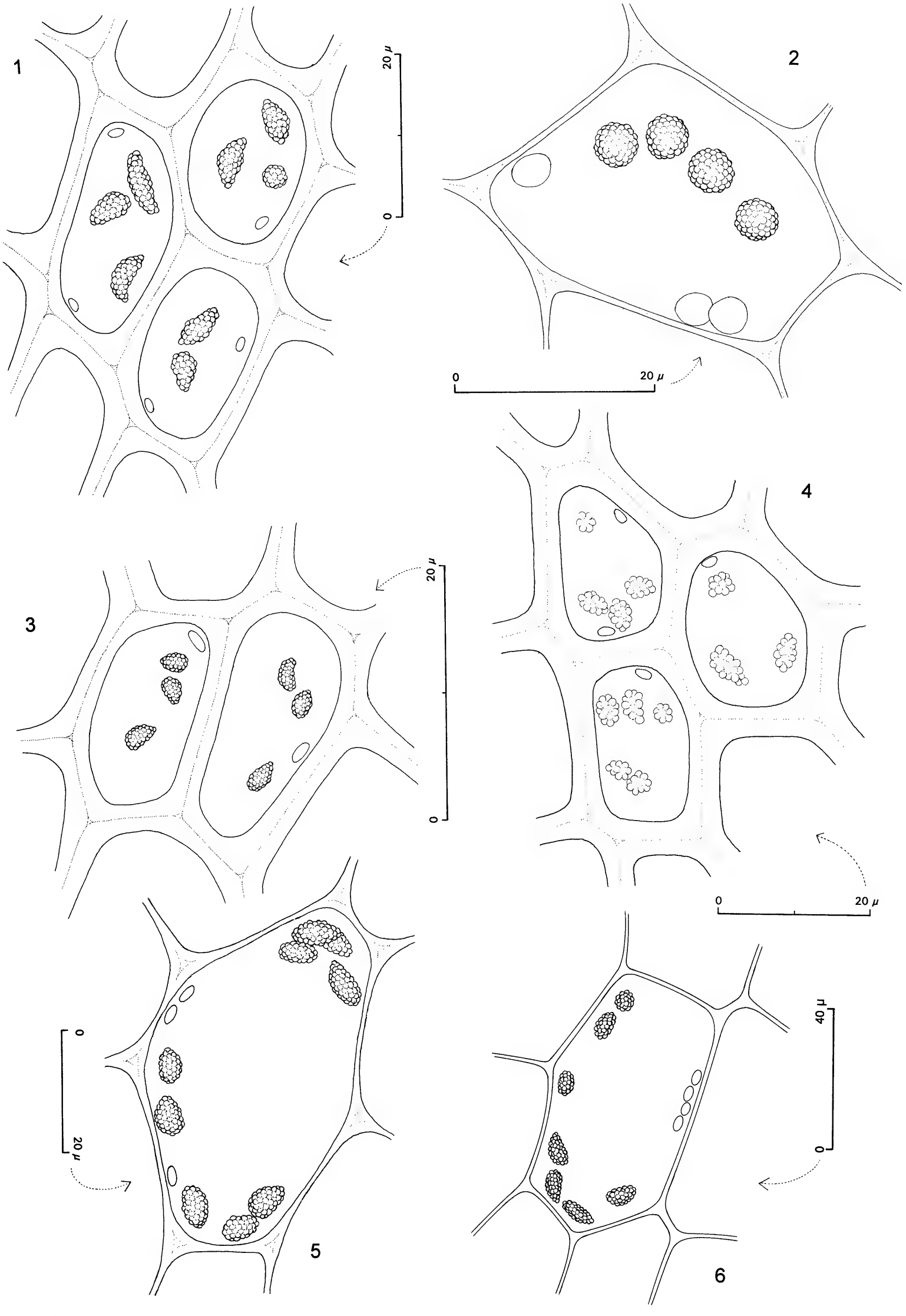

Fig. 50.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Lepidozia kirkii* Steph. Cells of upper sector of disc. 2. *Lepidozia digitata* Herzog. Cells of disc. 3. *Lepidozia ulothrix* (Schwägr.)

of stem cells, spreading, small, ca. 0.9–1× stem width, symmetrically 4-fid to 0.5 (median sinus), the lobes plane, slenderly acuminate, entire, terminating in a uniseriate row of 2–3(5) cells; disc 3–6 cells high at median sinus, the margins plane, entire.

Plants dioecious. Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series deeply concave, broadly ovate to ± orbicular; apices with 4 short lobes, the apical end of the marginal cells often diverging and forming a slight projection, the lobes thus crenulate; lamina margin bordered by cells of variable shape and orientation, the apical or free end of marginal cells variously divergent and forming a short projection or a tooth, the margin irregularly crenate-denticulate to the base; bracteole similar in size and form. Perianth long and prominent, slenderly cylindrical-fusiform, slightly curved, terete below, obscurely trigonous above, distinctly and deeply 3-plicate toward mouth, the perianth gradually narrowing toward the strongly contracted, shallowly 3-lobed mouth, the lobes composed of rather thick-walled, papillose cells that at the apical end are laterally free for varying lengths, the lobes crenate-denticulate.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (120–300 m), North Island (340–840 m), Chatham Islands (240 m). Known from Westland, Western Nelson, Auckland (Coromandel Forest Park, Waitakere Ra.) and Northland EPs.

Apparently primarily a lower-elevation species. In South Westland (Monkey Puzzle Gorge) the species occurred in a very protected niche: over soil deep in a pocket under a mass of fallen trees in a forest dominated by *Nothofagus menziesii* and *Dacrydium cupressinum*. At Lake Kaniere Scenic Reserve (Westland) the species occurs at 125 m in a mixed podocarp–broadleaf forest including narrow, shallow and stagnant pools with saturated, rich, peaty soil. At this site the vegetation consists of *Dacrydium cupressinum*, *Weinmannia racemosa*, *Podocarpus totara*, *Metrosideros umbellata* and an open understory dominated by *Pseudowintera colorata*, and *Lepidozia glaucescens* occurred loosely creeping over and among *Bazzania novae-zelandiae* or *Heteroscyphus decipiens* on the sides of bryophyte mounds. Also from beside a pool in a pakihi area under *Leptospermum scoparium*. Also known from a few sites in the North Island. In the Waipoua Forest in a wet forest dominated by *Weinmannia silvicola*, growing on the top of a bryophyte-covered log, as well as in *Agathis australis* forest with *Dacrydium cupressinum* and other podocarps, with an abundant ground tier of *Gahnia xanthocarpa*, where the species occurred in a shaded, protected niche on the ventral-lateral side of a log. Near the summit area of "Little Moehau" (Coromandel Forest Park, ca. 800–840 m) the species occurred in protected niches on vertical, shaded banks, in an area of rocky outcrops and shrub-heath communities including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus* and *Corokia buddleioides*. On Chatham Island it occurred on damp rocks and banks in a dense broadleaf forest, and on peaty soil in a clear-

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Lindenb. Upper disc cells. 4. *Lepidozia ulothrix* (Schwägr.) Lindenb. Upper disc cells. 5. *Telaranea gibbsiana* (Steph.) E.A.Hodgs. Upper disc cell. 6. *Telaranea tetrapila* var. *cancellata* (Colenso) J.J.Engel & Merrill. Median cell of disc. (Fig. 1, from *Glenny 9147*, New Zealand, South Is., Westland EP, Mt. Turiwhate, near summit; 2, from *Glenny 9083*, New Zealand, South Is., Canterbury EP, Mt. Aicken; 3, from *Glenny 9109*, New Zealand, South Is., Westland EP, Mt. Turiwhate; 4, from *Engel 27055*, New Zealand, South Is., Western Nelson EP, Kahurangi Natl. Park, Matiri Ra., Thousand Acres Plateau; 5, from *Glenny 9393*, Western Nelson EP, Brunner Ra.; 6, from *Engel 25127*, New Zealand, North Is., Auckland EP, Herangi Ra., Whareorino Forest.)

ing in *Dracophyllum arboreum – Corokia macrocarpa* treeland. Species recorded with *L. glaucescens* are *Hypnum chrysogaster*, *Kurzia hippuroides* and *Zoopsis argentea*.

Comments: *Lepidozia glaucescens* differs from the other glaucous-leaved species of the genus by having distinctly asymmetric leaves, with a ± straight dorsal margin (Fig. 49: 1, 3, 4, 7). The leaf cells and the cortical cells of the stem (in surface view) are distinctly thick-walled (Fig. 49: 11), rather than leptodermous as in *L. bisbifida* and *L. digitata*, and the wall thickenings have a distinctive lamellated (layered) appearance (Fig. 49: 10). The first branch underleaf is typically undivided in both *L. glaucescens* and *L. glaucophylla*.

The leaves of *Lepidozia glaucescens* are remarkable because of the unique combination of cells with discrete elliptical papillae and a ± uniform waxy, granular coating (Fig. 49: 10). The papillae are hemispherical to short on the lobes (Fig. 49: 10), but distinctly elongate in the median and basal sectors of the disc (Fig. 49: 11). The waxy coating is poorly developed in many collections, however, and is often evident only on the new growth at the tips of the shoots. Consequently, *L. glaucescens* might be mistaken for *L. novae-zelandiae*, which also has a striate-papillose surface, similar leaf shape, and lobes terminating in a differentiated uniseriate row of elongated, thick-walled cells. Under the compound microscope, however, the leaf surface of *L. glaucescens* has a semiopaque, granular appearance, even if the waxy coating is not apparent under the dissecting microscope.

Plants with an apparently smooth surface but possessing ± flat discs with spreading lobes, ± straight dorsal margin of the leaf, and thick-walled lobe and disc cells should be determined with great care. Some populations of the species have surface papillae suboptimally developed, and several leaves from various areas of, preferably, several shoots should be examined (including leaves from near the shoot apex). Verification under oil-immersion is at times helpful.

Telaranea Spruce *ex* Schiffn.

Telaranea Spruce *ex* Schiffn. *in* Engl. & Prantl, Nat. Pflanzenfam. 1(3,1): 103. 1893, *nom. cons.*
Telaranea Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 358, 360, 365. 1885, *nom. inval. in syn.*
Lepidozia subg. *Telaranea* (Spruce *ex* Schiffn.) Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland 6(2): 276. 1914.
Arachniopsis Spruce, Cephalozia 84. 1882, *nom. rejic.*
Neolepidozia Fulford & J.Taylor, Brittonia 11: 81. 1959.
Acrolepidozia R.M.Schust., J. Hattori Bot. Lab. 26: 254. 1963.

Plants soft-textured and often lax, to ± stiff and wiry, to thread-like and minutely prickly, mostly prostrate or creeping, occasionally ascending to suberect, pale, whitish or yellowish to pure green, rarely brownish yellow to rust-brown, often nitid, at times glaucous and water-repellent. Branching 1(2)-pinnate, usually rather regularly so, the branches predominantly of *Frullania* type, rarely to frequently becoming flagelliform, rarely absent; *Microlepidozia*-type and *Acromastigum*-type branches in some species; ventral-intercalary branches present, leafy or stoloniform, or absent; lateral-intercalary branches rarely present. Stems with 9–18 rows of cortical cells (as few as 4 in some species of sect. *Tenuifoliae*), mostly thin-walled, forming a conspicuous hyaloderm (up to 30 rows of weakly differentiated cells in sect. *Tricholepidozia*); medullary cells numerous (few in some species of sect. *Tenuifoliae*). Rhizoids from basal and/or distal cells of underleaf. Leaves incubously inserted and oriented, varying to transversely inserted or almost longitudinal in some species, rarely weakly succubous, highly variable in form, ± symmetrically lobed, in most species 4-lobed or 4–6-lobed, but sometimes 2–3-lobed, occa-

sionally simple or 12-lobed (sect. *Tricholepidozia*), the leaves shallowly to deeply divided. Lobes ranging from acute, caudate, acuminate to ciliiform, typically uniseriate for much of their length, to uniseriate almost or quite to the base. Disc (when present) variable, from 2 cells high (consisting of a single tier of cells along the insertion, plus the basal cells of the lobes) to as many as 6(14) cells high, in some species the "disc" consisting of the connate basal cells of the lobes; margins normally entire (very rarely denticulate by projecting septa). Cells of disc typically in regular rows and tiers, the number of cell rows equal to twice the number of lobes, often large, usually leptodermous, occasionally firm- to evenly thick-walled, often rather turgid, in a few species collapsing on drying; surface mostly smooth, in some species variously papillose, finely scabrous (with minute, sharp prickles), or with a uniform glaucous coating. Oil-bodies hyaline or greyish, the surface variable, ± homogeneous in some species, coarsely granular in other species, some species coarsely papillose, (4)5–9(12) per cell. Underleaves small and inconspicuous to large and similar to leaves in form but with fewer and often shorter lobes; margins entire. Asexual reproduction rare, by tubers or caducous and fragmenting leaf lobes in a few species.

Dioecious, less commonly autoecious. Androecia either terminal on short to moderately long *Frullania*-type branches or, more often, on short, spicate ventral-intercalary branches from leading shoots; bracts typically monandrous, the antheridial stalk 1- or 2-seriate; bracteolar antheridia lacking. Gynoecia on short ventral-intercalary branches lacking normal vegetative leaves. Bracts and bracteoles similar, crenulate to dentate, lobulate to shallowly to deeply lobed. Perianth large for plant size, typically assurgent, ovoid to fusiform to cylindrical, terete below, usually bluntly trigonous to shallowly to deeply plicate above (rarely eplicate), gradually or abruptly narrowed to the mouth; perianth mouth variable, denticulate to shallowly lobulate to lobulate-ciliate to subfimbriate; perianth 2–4(5)-stratose in basal portion, the median portion (1)2(3)-stratose.

Seta with outer layer of 8 cells or exceptionally as few as 4, the inner cells 15–24(34) to 12 or fewer, rarely as few as 6 or 4. Capsule short- or exceptionally long-ellipsoidal, the wall typically 3-stratose, less often 2-, 4-, or 5-stratose; outer layer of cells in tiers, rectangular, with two-phase development, the longitudinal walls with nodule-like thickenings alternating with primary walls devoid of thickenings; innermost cells usually with semiannular bands, the bands complete, less often incomplete, or bands weakly developed or lacking, the radial walls with nodular thickenings and short spine-like extensions onto the exposed tangential wall.

Spores (SEM) reticulate-areolate, with enclosed polygonal areolae bounded by a network of low ridges, or papillose-vermiculate, with short discontinuous ridges formed by coalesced papillae, or the surface irregularly roughened. Elaters little tapered, typically bispiral to tips.

Type: *Lepidozia chaetophylla* Spruce

Telaranea with 98 species according to Engel and Merrill (2004) is the third largest genus of *Lepidoziaceae*, after *Bazzania* and *Lepidozia*. Engel and Merrill (2004) recognized two subgenera, subg. *Acrolepidozia* and subg. *Telaranea*, and seven sections within subg. *Telaranea*, sect. *Neolepidozia* (Fulford & J.Taylor) J.J.Engel & Merrill, sect. *Cancellatae* J.J.Engel & Merrill, sect. *Ceraceae* J.J.Engel & Merrill, sect. *Tricholepidozia* (R.M.Schust.) J.J.Engel & Merrill, sect. *Transversae* J.J.Engel & Merrill, sect. *Telaranea* and sect. *Tenuifoliae* (R.M.Schust.) J.J.Engel & Merrill. Representatives of all subgenera and sections occur within our area; 25 species occur in New Zealand. The phylogenetic analysis in Engel and Merrill (2004) indicated that *Kurzia*, as defined by the presence of *Microlepidozia*-type branching, is polyphyletic, and the following species and variety previously assigned to *Kurzia* were transferred to *Telaranea*: *K. quadriseta*, *K. quadriseta* var. *trilobata*, *K. fragilifolia* and *K. quinquespina*.

Taxa with 4-lobed leaves may be confused with those of *Lepidozia*. The experienced student, however, will soon come to separate the two genera on the basis of surface texture (*Telaranea* is often or usually somewhat to strongly nitid; *Lepidozia* species are all dull-textured) and degree of firmness (*Telaranea* species, even the larger, are soft-textured, more gracile, sometimes silky, sometimes delicate; cells in at least the lobes often collapse in drying). *Lepidozia* species are firm-textured; their cells never collapse in drying.

The genus includes a diversity of elegant and in many cases beautiful plants. The species of *Telaranea* seem, at first glance, to belong to wholly different genera, and indeed, until recent decades were assigned partly to *Lepidozia*, partly to *Neolepidozia*, and only in small part to *Telaranea s. str.* (see Engel and Merrill, 2004).

References: Engel and Merrill (2004); Hodgson (1956; *sub Lepidozia*); Schuster (2000a).

Key to Species

1a. Leaves and underleaves with 2–6 lobes; stem with a distinct hyaloderm formed of 6–18 cell rows; capsule wall normally 2–4-stratose 2

2a. Leaves (on main shoots) with 4 or more lobes (or if 3-lobed, then with disc present); leaf disc present and variously developed, 2–6 (to 9) cells high, or in deeply divided leaves, with at least one tier of disc cells along the insertion, plus the basal cells of the lobes; leaf lobes 2–4(8) cells wide at base; half-leaf associated with terminal branches with 2 or more lobes (undivided in *T. fragilifolia* and *T. martinii*) 3

3a. Lobes caudate, with a broad triangular base abruptly contracted to a uniseriate row, the cells of the uniseriate row distinctly elongated (ca. 4–5:1) and capillary; lobe cells thick-walled in comparison to the cells of the disc, the septa thickened in the corners and swollen. North Is. and Western Nelson. . . . . *T. gibbsiana* (p. 291)

3b. Lobes acute, gradually attenuate to acuminate, the lobe cells shorter (to 3:1, except *T. elegans*); lobe cell walls ± equal in thickness to those of disc cells, the septa often thickened in the corners but not swollen (except *T. praenitens*) 4

4a. Plants glaucous and water-repellent; lobe tips (and sometimes disc) fragmenting. 5

5a. Disc cells thin- to firm-walled, larger, to 54 µm wide; disc and lobe margins not denticulate; plants whitish, glaucous, larger (to 1 cm wide with branches) 6

6a. Underleaf disc 3–4 cells high; leaf disc margins entire (cells not bulging). Primarily South Is. . . . . *T. tuberifera* (p. 312)

6b. Underleaf disc 1–2(3) cells high; leaf disc margins crenulate by bulging cells. North Is.. . . . . *T. perfragilis* (p. 315)

5b. Disc cells uniformly thick-walled, smaller, to 45 µm wide; disc and lobe margins finely denticulate by projecting upper ends of cells; plants green to olive, ± nitid, often glaucous only in youngest parts of plant, small (to 6 mm wide with branches). North Is.. . . . *T. elegans* (p. 309)

4b. Plants not glaucous; lobe tips persistent 7

7a. Disc 14–16 cells wide at the insertion (or if ca. 8, then the disc more than 6 cells high), the leaves often ± horizontally inserted and oriented; leaf lobes (4)5–6(8) cells wide at base; cells of disc and lobes ± undifferentiated 8

8a. Disc narrowing to 8(9) cells wide at the insertion; stem cortical cells in 12–14 rows; leaves asymmetrically lobed, the dorsal lobe shortest, the 2 ventral lobes largest, somewhat paired and often subfalcate (especially on branches). Median leaf cells 16–26 mm wide, evenly thick-walled and firm. Westland Prov. . . . . *T. pennata* (p. 279)

8b. Disc (11)14–16(18) cells wide at insertion; stem cortical cells in ca. 24 rows; leaves ± symmetrically lobed. Hygric, often in bogs. Auckland Is., South Is., unknown north of Westland Prov. . . . . *T. meridiana* (p. 276)

7b. Disc typically 8 cells wide at the insertion (6 cells wide in 3-lobed leaves), the leaves transversely to incubously inserted (if horizontally oriented, then leaves glaucous, cf. couplet 4); leaf lobes 4 cells wide at base or fewer; cells of disc and lobes variously differentiated (in size, shape, wall thickening and surface). 9

9a. Stem leaves all or predominately 3-lobed (or if 4-lobed, then plants distinctly glass-like when dry, and appearing etiolated, the leaves shrunken). 10

10a. *Microlepidozia*-type branches present; underleaves asymmetrically 3–4-lobed, with one or more lobes abbreviated 11

11a. Leaves with lobes persistent, the leaves of main stems 3(4)-lobed, the disc 2–3 cells high; branch leaves mostly 3-lobed; leaf surface smooth or finely striate-papillose. Lateral-intercalary branches occasional. Stewart Is., South Is., North Is. . . . . *T. trilobata* (p. 333)

11b. Leaves with lobes freely fragmenting, the leaves on main stems all 3-lobed, the disc 1–1.5 cells high; branch leaves asymmetrically bifid (dorsal lobe shorter); leaf surface striolate. North Is., Little Barrier Is. . . . . *T. fragilifolia* (p. 334)

10b. *Microlepidozia*-type branches absent; underleaves symmetrically lobed (or if asymmetric, 2-lobed, the longer lobe uniseriate, resembling the lobes of the leaves 12

12a. Leaf disc 1.5 cells high, with a single tier of cells along the insertion, plus the partially connate basal cells of the lobes; surface of leaf lobes minutely scabrous; first branch underleaf undivided. North Is. . . . . *T. granulata* (p. 344)

12b. Leaf disc 2–4(5) cells high; surface of leaf lobes finely striate-papillose (*T. remotifolia*) or smooth; first branch underleaf bilobed, often asymmetrically 13

13a. Leaves 3–4-lobed, shrunken and glass-like when dry, the lobes often sharply decurved and claw-like; branch half-leaf bilobed; stems fleshy, with cortical cells in 10–13 rows, the medullary cells in 17–25 rows; dioecious. Sporadic on South and North Is. . . . . *T. remotifolia* (p. 316)

13b. Leaves on main shoot consistently 3-lobed, the lobes ± straight, not claw-like; branch half-leaf undivided; stems slender, with 9 cortical cells, the

medullary cells in 9–10 rows; monoecious. Widespread but sporadic . . . . . *T. martinii* (p. 339)

9b. Stem leaves 4–6-lobed, never 3-lobed on main shoots; plants not glass-like, not etiolated in aspect, the leaves not appearing shrunken. Lobes not claw-like, about equal in size 14

14a. Leaf disc 1.5–3(4) cells high 15

15a. Basal tier of disc cells small, short-rectangular to quadrate; *Microlepidozia*-type branches present; underleaves asymmetrically lobed, with 1 or more lobes abbreviated . . . . . *T. pallescens* (p. 331)

15b. Basal tier of disc cells narrowly elongate; *Microlepidozia*-type branches not produced; underleaves symmetrically lobed 16

16a. Disc of stem leaves (including basal tier of lobe cells) 2 (rarely 3) cells high; cells of uniseriate row of leaf lobes straight-sided and without or with weakly protruding septa, the cells thicker-walled than those of disc; leaves (except var. *complanata*) of both stems and branches widely spreading to squarrose, typically transversely inserted and oriented (branch leaves at times weakly incubous); stem medullary cells thick-walled, in 40–67 rows; branches (except var. *complanata*) terete; sporophytes common. Common throughout New Zealand . . . . . *T. lindenbergii* (p. 324)

16b. Disc of stem leaves 3(4) cells high (rarely 2); cells of uniseriate row of leaf lobes typically constricted at the septa, the cells not noticeably thicker-walled than those of disc; leaves of both stems and branches obliquely spreading, incubously inserted and oriented; stem medullary cells thin-walled, in 18–36 rows; branches complanate; sporophytes unknown. Primarily South Is. . . . . *T. tetradactyla* (p. 336)

14b. Leaf disc 4 or more cells high from medium sinus base to leaf base 17

17a. Leaves densely areolate, the cells small (18–40 mm wide in median disc), never turgid and pillow-like, typically firm-walled, trigones often present, small to medium 18

18a. Cells of uniseriate row of leaf lobes with septa thickened and projecting; disc margins (especially the dorsal) minutely serrulate by projecting distal ends of cells. Surface of lobe cells finely to distinctly striate-papillose. Widespread in New Zealand . . . . . *T. praenitens* (p. 285)

18b. Cells of uniseriate row of leaf lobes with septa thickened but not distinctly swollen and projecting; disc margins entire 19

19a. Disc cells small, the largest to 25 mm wide, the areolation dense, the cells somewhat irregularly arranged; branches complanate, wider than the main shoot, the branch leaves typically closely and regularly shingled. Campbell and Auckland Is. (rare) . . . . . *T. tridactylis* (p. 281)

19b. Disc cells larger, the largest to 40 μm wide, the areolation more ordered and regular (cells in ± regular rows and tiers); branches not complanate, the branch leaves not tightly shingled. Disc cells with small but distinct trigones; lobes about equal to or shorter than the disc, the uniseriate row 2–4(5) cells long (typically less than half the length of lobe). Auckland, Campbell and Stewart Is., rather common throughout South Is. and North Is. . . . . *T. patentissima* (p. 295)

17b. Leaves laxly areolate, the cells larger (40 μm or more wide in median disc), often appearing turgid and distinctly pillow-like (even under low magnification), typically ± thin-walled and with trigones lacking 20

20a. Leaves (disc) ± symmetrical; leaf lobes acute to acuminate, with 1–2 tiers of paired cells at base; disc cells isodiametric 21

21a. Cells in median sector of disc thin-walled, to (45)50–70 mm wide; uniseriate portion of leaf lobe 5–6 cells long; plants varying from medium to robust (to 1.5 cm wide), highly nitid; disc weakly to distinctly cuneate and (9)14–21 cells broad distally (approaching 8 cells wide throughout in var. *roseana*). Common . . . . . *T. tetrapila* (p. 301)

21b. Cells in median sector of disc evenly thick-walled and firm, rather dense, to 38 μm wide; uniseriate portion of leaf lobe short, 2–3 cells long; plants small and stenotypic in stature, ca. 0.6 cm wide (including branches), rather dull; disc subquadrate, 8(9) cells wide throughout. Auckland Is., South Is. and extreme southern sector of North Is. . . . . *T. hodgsoniae* (p. 293)

20b. Leaves (disc) asymmetrical; leaf lobes long-attenuate, often falcate and hooked at the tips, with 3–5 tiers of paired cells at base; disc cells ± elongate . . . . . *T. paludicola* (p. 307)

2b. Leaves with 2–3 lobes, deeply divided; leaf "disc" formed of the partly connate basal lobe cells and lacking a tier of disc cells along the insertion; leaf lobes from a uniseriate or biseriate base; half-leaf undivided 22
22a. Stems appearing fleshy, the cortex in 9–10 cell rows and the medulla in 18–24 rows; leaf lobe bases biseriate, the paired cells elongate, connate for more than 0.5 their length, the cells of the uniseriate row barrel-shaped, constricted at septa; underleaves 3–4-lobed. Alpine tussockland plant . . . . . *T. nivicola* (p. 343)
22b. Stems slender and wiry, the cortex in 6–9 cell rows and the medulla in 6–12(18) rows; leaf lobes uniseriate or biseriate at base, the basal cells connate for 0.1–0.4 their length, the cells of the uniseriate row with septa thickened at the corners, feebly swollen; underleaves bilobed. Lowland plants 23
23a. Underleaves typically asymmetrically bilobed, the longer lobe resembling a leaf lobe, with a uniseriate row 4(5) cells long, the other abbreviated, with a pair of short basal cells, a ± elongated cylindrical cell, capped by a slime papilla; *Microlepidozia*-type and lateral-intercalary branches present . . . . . *T. quinquespina* (p. 347)
23b. Underleaves symmetrically bilobed, small and caliper-like; *Microlepidozia*-type and lateral-intercalary branches absent 24
24a. Lobes not tapering, flexuous, 6–9 cells long; first branch underleaf equally and symmetrically bilobed; leaves consistently bilobed, the lobes unequal in length; lobe cells about equal in length, the terminal cell small and button-like; cortical cells moderately and evenly thick-walled. Rare. . . . . *T. inaequalis* (p. 357)
24b. Lobes tapering, stiff, (4)5–6 cells long; first branch underleaf asymmetrically bilobed, one lobe long and divergent, the other short and appressed, resembling an underleaf lobe; leaves 2–3-lobed, when bilobed the lobes ± equal in length; lobe cells gradually shorter toward tip, the terminal cell not small and button-like; cortical cells thin-walled. Rather common. . . . . *T. herzogii* (p. 350)
1b. Leaves with 8–12(13) lobes; stem with a weakly differentiated hyaloderm of ca. 24–28 cell rows; capsule wall 5-stratose. Stewart Is., Southland and Westland provinces . . . . . *T. pulcherrima* (p. 319)

Subg. ***Acrolepidozia*** (R.M.Schust.) R.M.Schust.

Acrolepidozia R.M.Schust., J. Hattori Bot. Lab. 26: 254. 1963. *Telaranea* subg. *Acrolepidozia* (R.M.Schust.) R.M.Schust., J. Hattori Bot. Lab. 36: 389. 1973 (1972). *Telaranea* subg. *Acrolepidozia* (R.M.Schust.) R.M.Schust., Hepat. Anthocerotae N. Amer. 2: 30. 1969, *nom. inval. basionym non cit.*

Telaranea sect. *Latifoliae* J.J.Engel & Merrill, Phytologia 79: 251. 1996 (1995). Type: *Lepidozia meridiana* Hodgs.

Telaranea meridiana (E.A.Hodgs.) E.A.Hodgs.

[Fig. 51]

Lepidozia meridiana E.A.Hodgs., Trans. Roy. Soc. New Zealand 83: 611. *pl. 2, f. 24*. 1956. *Telaranea meridiana* (E.A.Hodgs.) E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. Type: Auckland Is., "Cape Expedition," No. 2 Camp, 31 Oct. 1944, *Turbott s.n.* (CHR!); isotype: (MPN, *non vidi*).

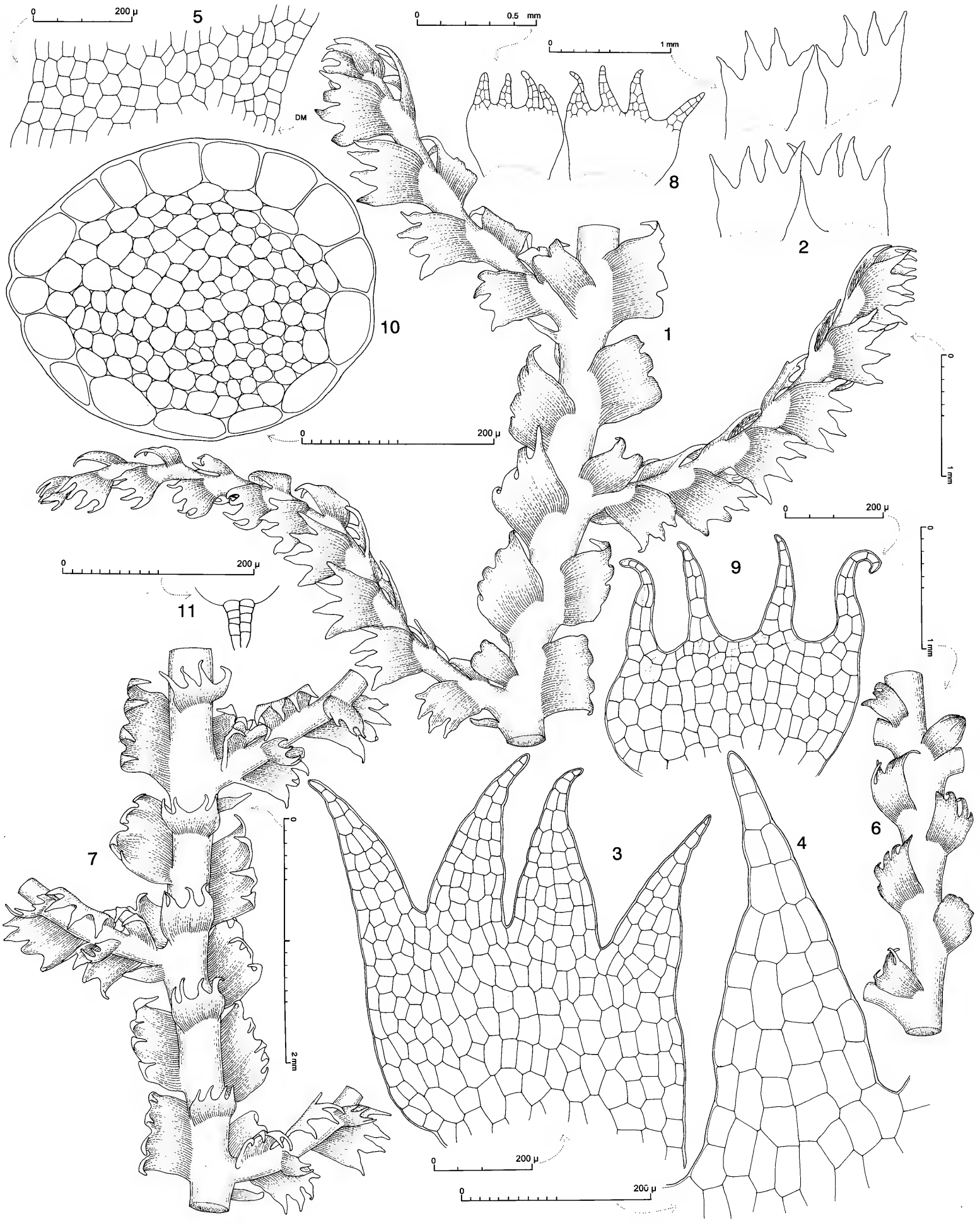

Fig. 51.
Telaranea meridiana (E.A.Hodgs.) E.A.Hodgs. 1. Sector of main shoot, dorsal view. 2. Leaves. 3. Leaf, cellular detail. 4. Leaf lobe. 5. Leaf base (DM = dorsal margin). 6. Shoot sector of vigorous plant, dorsal view. 7. Sector of main shoot, ventral view. 8. Underleaves. 9. Underleaf, cellular detail, stippled cell walls indicate rhizoid initials. 10. Stem, cross section. 11. Antheridial stalk. (Figs. 1–4, 7–10, from type; 5, from *Johnson 175*, New Zealand, South Is., Fiordland EP, Lake Manapouri; 6, from *Child H3669*, New Zealand, South Is., Westland EP, Mahinapua; 11, from *Child H3101*, New Zealand, South Is., Otago EP, Mt. Cargill.)

Plants soft and flexuous, brittle, ascending to suberect, in dense cushions, pale green, nitid when dry; shoots medium, to 1.3 cm wide, including branches. Branching somewhat regularly but loosely 1(2)-pinnate, the branches typically flexuous and somewhat contorted, of the *Frullania* type; branch half-leaf bifid, narrowly rectangular, the lobes ± parallel; first branch underleaf undivided, broadly acuminate (rarely bilobed), inserted on ventral-lateral side of branch at juncture of branch and main axis, grading to longitudinally inserted on stem just below the branch. Ventral-intercalary branches not seen. Stems with cortical cells rather weakly (on strongest main axis) to distinctly differentiated, thin-walled, in 17–24 rows; cortical cells in section slightly to distinctly larger than the numerous (ca. 120) medullary cells. Leaves on main shoot rigid, widely spreading, distant to contiguous (on compact shoots), the disc plane or nearly so, rarely convex, the lobes ventrally decurved and claw-like (not visible in dorsal view), the insertion incubous (on elongated main shoots the leaves often strongly longitudinally inserted and oriented, with the disc broader than high and nearly in same plane as dorsal surface of stem); leaves 520–700 μm wide × 545–770 μm long, the leaves 4(6)-lobed to 0.4–0.6, the lobes slightly shorter than the disc. Lobes weakly acuminate, the largest leaf lobes (4)5–6(8) cells wide at extreme base, 4–5 cells wide for 4–5 tiers, biseriate for 1–2 tiers, terminating in a short uniseriate row of 2–3(4) cells; lobe cells ± isodiametric to short-rectangular, thin-walled, the cell walls of the uniseriate row not or very weakly thickened in the corners; surface smooth, rarely feebly striate-papillose. Disc moderately asymmetrically rectangular, the dorsal margin longer than the ventral, 6–8 cells high (from median sinus base to leaf base), 21–24 cells wide in distal portion narrowing to (11)14–16 cells wide in basal portion; dorsal margin straight or weakly subcordate at the base, the ventral straight. Cells of disc thin-walled, trigones lacking, the median cells elongate, 30–42 μm wide × 38–51 μm long, the cells in ± irregular rows; basal row of disc cells somewhat larger; surface smooth. Underleaves much smaller than leaves, ca. 1–1.2× stem width, strongly spreading, distant, plane, 4(6)-lobed to 0.35–0.65, the lobes acuminate, 3–4 cells wide for 1–several tiers at base and biseriate for 2–3 tiers, ending in 2 laterally juxtaposed cells, or more commonly in a uniseriate row formed of 2(3) short cells, terminating in a slime papilla; disc symmetrically subrectangular (wider than high), 5–6 cells high (median sinus), 15–18 cells wide at widest point, the cells ± regularly arranged. Rhizoid initial cells small, subquadrate, forming a continuous bistratose pad or band often including the basal portion of the lobes as well as the apex of the disc. Asexual reproduction lacking.

Plants dioecious. Androecia either on short *Frullania*-type branches with a few cycles of reduced leaves prior to androecial formation, or on short, abbreviated, ventral-intercalary branches from leading shoots; bracts dorsally assurgent, deeply concave, 2-lobed, the lobes acuminate, terminating in a uniseriate row of 2 not or hardly elongated cells; lamina cells irregular in arrangement, the dorsal margin of lamina feebly dilated and slightly incurved, entire or crenulate, devoid of slime papillae; bracts monandrous; antheridial stalk biseriate; bracteolar antheridia absent. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands, Stewart Island (125 m), South Island (0–610 m). Known from Fiordland, Otago and Westland EPs, not known north of Greymouth.

The species occurs at lower to median elevations, and is primarily terricolous in damp or boggy sites on the forest floor. It less commonly is found in rather open sites, such as in low, mucky niches in swampy areas with *Sphagnum* and scattered *Leptospermum scoparium*, at sea level just north of the Haast River. At Ship Creek (near Haast River, Westland) it grows in low, wet areas just above the water level in a mature *Dacrycarpus dacrydioides* swamp forest.

In the Lake Kaniere area (Westland, 125 m) the species is very common on saturated, rich, peaty soil in and especially at the edges of narrow, shallow, ± stagnant pools in the shade of a mixed podocarp–broadleaf forest. Vegetation at this site consists of *Dacrydium cupressinum*, *Weinmannia racemosa*, *Podocarpus totara*, *Metrosideros umbellata* and an open understory dominated by *Pseudowintera*. It also occurs in pakihi under rushes, etc., associated with *Sphagnum*. The species is associated with a variety of other hepatics that occur in forest niches, e.g., *Lepidozia procera*, *L. laevifolia*, *L. spinosissima* and *Telaranea tetradactyla.*

Comments: Particularly diagnostic for this distinctive species are the flexuous, rather loosely pinnate shoots, and the broad-based, longitudinally inserted and oriented leaves (particularly on elongated main shoots, Fig. 51: 1), which may be up to 16 cells wide in the basal sector. Also distinctive are the broad lobes, (4)5–6(8) cells wide at base, which are ventrally decurved and claw-like, and the uniform, dense areolation of the disc and lobes. In more compact expressions, however, the insertion is variable, from distinctly to rather weakly incubous, and the leaves are rather markedly convex (Fig. 51: 6).

Subg. ***Telaranea***

Telaranea sect. *Neolepidozia* (Fulford & J.Taylor) J.J.Engel & Merrill, Fieldiana, Bot. 44: 17. 2004. *Neolepidozia* Fulford & J.Taylor, Brittonia 11: 81. 1959. *Telaranea* subg. *Neolepidozia* (Fulford & J.Taylor) R.M.Schust., J. Hattori Bot. Lab. 26: 255. 1963. *Lepidozia* sect. *Neolepidozia* (Fulford & J.Taylor) Piippo, Ann. Bot. Fennici 21: 314. 1984.

Telaranea pennata J.J.Engel & Merrill

[Fig. 52]

Telaranea pennata J.J.Engel & Merrill, Phytologia 79: 252. June 1996 (1995). Holotype: New Zealand, South Is., Westland Prov., Route 73, 8 miles W of Turiwhate, *Engel 6754* (F); isotype: (CHR).

Plants rather stiff, loosely prostrate, loosely matted, pale green to olive-green, nitid when dry; plants medium, to 1 cm wide, including branches. Branching very regularly 1-pinnate, the branches of the *Frullania* type, rather long for plant size; branch half-leaf bifid, narrowly rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided, subulate, (rarely bilobed) inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, becoming leading leafy shoots. Stems with cortical cells distinctly differentiated, rather thick-walled, in 12–13 rows; cortical cells in section much larger than the numerous (ca. 80) medullary cells. Leaves on main shoot rigid, obliquely spreading, contiguous to imbricate, the disc ± plane, the lobes somewhat ventrally deflexed, the insertion strongly incubous; leaves 330–390 μm wide × 315–435 μm long, moderately asymmetric (the dorsal margin shorter), 4(5)-lobed to 0.4–0.45, the lobes shorter than the disc. Leaves on branches closely and regularly imbricate, the ventral lobes subfalcate, appearing as if brushed toward shoot apex. Lobes acute to weakly acuminate, the dorsal lobe shortest, the 2 ventral lobes largest, somewhat paired and often subfalcate (especially on branches), the largest leaf lobes (4)5–8 cells wide at extreme base, terminating in a short uniseriate row of 2–4 cells (ca. half or less the length of lobe); lobe cells short, ± isodiametric to short-rectangular, thick-walled, the cell walls of uniseriate row somewhat thickened in the corners but the septa not

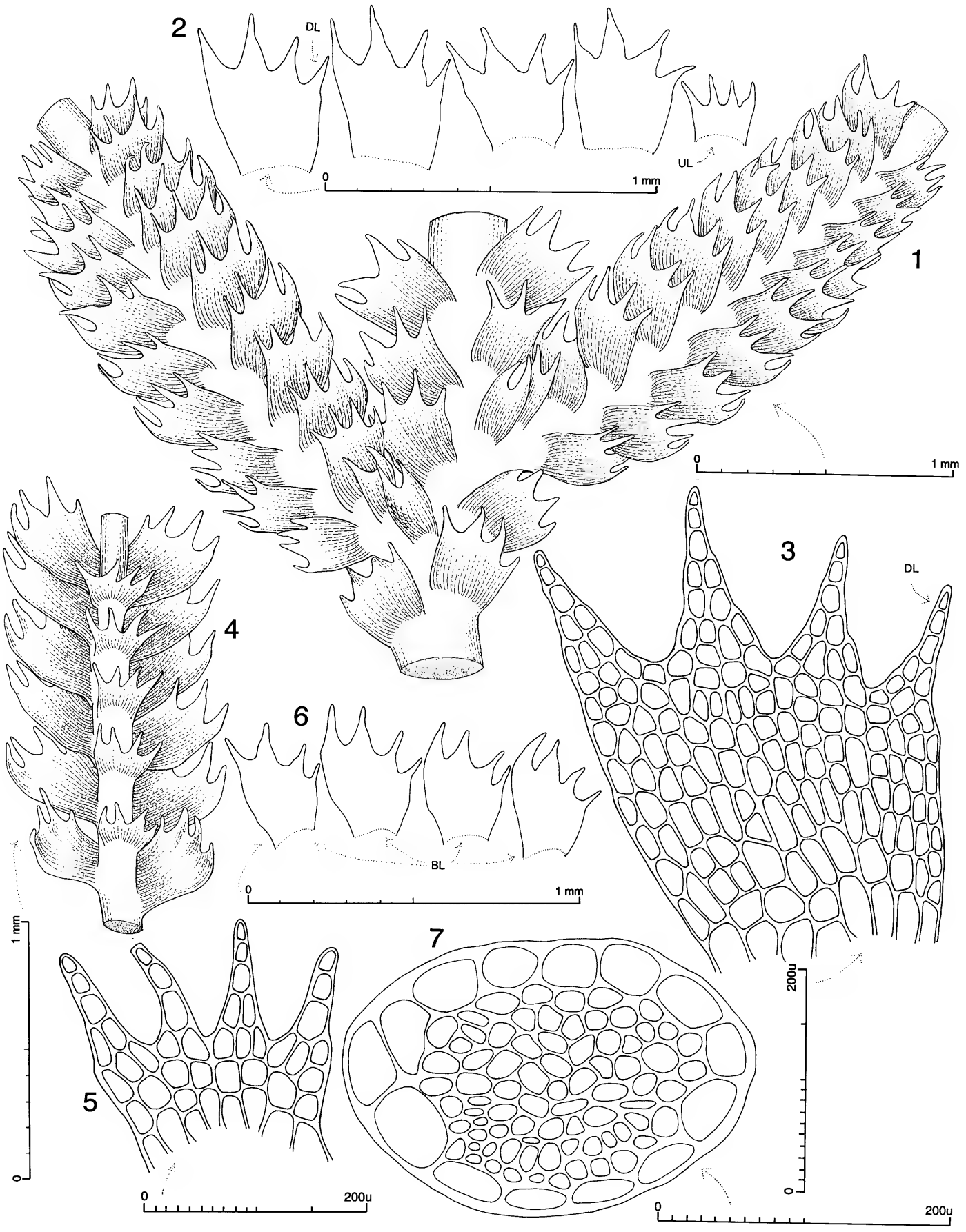

Fig. 52.
Telaranea pennata J.J.Engel & Merrill. 1. Sector of main shoot with *Frullania*-type branches, dorsal view. 2. Leaves (dorsal lobe [= DL] at right) and to right an underleaf (= UL). 3. Leaf, cellular detail (DL = dorsal lobe). 4. Sector of branch, ventral view. 5. Underleaf, cellular detail. 6. Branch leaves (= BL; dorsal lobe at right). 7. Stem, cross section. (All from holotype.)

swollen and projecting at the lobe margin; surface smooth to finely striate-papillose at lobe tips. Disc subsymmetrically quadrate-rectangular to obliquely trapezoidal, 6–9 cells high (8–10 cells high in branch leaves), 16–19 cells wide in distal portion narrowing to 8–9 cells wide in basal portion; dorsal margin straight to weakly incurved, the ventral rounded. Cells of disc small, evenly thick-walled and firm, trigones lacking, the median cells elongate, 16–26 μm

wide × 30–40 μm long, often elongated longitudinally, following the contour of the leaf; basal row of disc cells larger (especially in ventral-basal sector); surface smooth. Underleaves much smaller than leaves, 0.9–1× stem width, strongly spreading, distant, plane, 4-lobed to 0.5–0.6, the lobes somewhat divergent, narrowly acuminate, the uniseriate portion formed of 3–4 short cells, terminating in a slime papilla; disc symmetrically subrectangular (wider than high), 3(4) cells high (median sinus), the cells ± regularly arranged, the disc 8 cells wide. Asexual reproduction lacking.

Androecia and gynoecia not seen.

Distribution and Ecology: Known only from the type locality, a dryish forest in Westland, where the species occurs both over rock and fallen logs in a streambed.

Comments: The species may be immediately distinguished by the highly regular, neatly combed appearance of the branches (Fig. 52: 1) and the characteristic asymmetry of the leaves—the dorsal lobe shortest, and the ± paired ventral lobes appearing brushed toward the branch tips (Fig. 52: 3, 4). Many of our *Telaranea* taxa have asymmetrical *Lepidozia*-like leaves (e.g., *T. paludicola*), with the dorsal lobes paired and often distinctly larger than the ventral. The leaves in *T. pennata*, however, are almost a mirror image of the typical *Lepidozia*-type leaf. Also, the leaf lobes in *T. pennata* are broader than in any other New Zealand *Telaranea* (up to 8 cells wide at the base).

Telaranea tridactylis (Lehm. & Lindenb.) J.J.Engel & Merrill

[Figs. 53, 54]

Jungermannia tridactylis Lehm. & Lindenb. *in* Lehm., Nov. Min. Cogn. Stirp. Pug. 4: 41. 1832. *Lepidozia tridactylis* (Lehm. & Lindenb.) Mont. *in* Dumont d'Urville, Voy. Pôle Sud, Bot. 1: 245. 1845. *Telaranea tridactylis* (Lehm. & Lindenb.) J.J.Engel & Merrill, Phytologia 79: 253. June 1996 (1995). Type: "Nova Hollandia," without specific loc., *sin. coll.*, "Hb. Berol[inensis] 46" (W!, Lindenberg Hepat. no. 4636).

Lepidozia oldfieldiana Steph., Sp. Hepat. 3: 581. 1909, *syn. nov*. Lectotype (*fide* Engel and Merrill, 2004): Tasmania, without specific loc., *Oldfield*, ex herb. Kew (G! – *c.* ♂).

Plants rather stiff and wiry, prostrate in compact mats, light olive-green, highly nitid when dry, not water-repellent; shoots very small for subgenus, the main shoots 350–560 μm wide (0.5 cm wide with branches). Branching irregularly to regularly 1-pinnate, occasionally locally 2-pinnate, the branches of the *Frullania* type; branch half-leaf bifid, the lobes sometimes widely divergent; first branch underleaf undivided, subulate, inserted on ventral or ventral-lateral side of branch near juncture of branch and main axis. Ventral-intercalary branches common, leafy or sporadically flagelliform. Stems with cortical cells in 12–13 rows, often rather thick-walled and firm in surface view; medullary cells in ca. 38 rows, the cells much smaller than cortical cells. Rhizoids sparse, from distal cells of underleaf disc. Leaves on main shoot rigid, fragile, widely spreading, but not at right angles to stem, loosely imbricate to conspicuously distant, plane or slightly concave resulting from occasional gentle incurving of lobes, the insertion variable: subtransverse to strongly incubous to almost longitudinal; leaves (145)265–385 μm wide × (120)235–335 μm long, subsymmetric, 4-lobed (rarely 5–6-lobed) to 0.45–0.6, the lobes moderately to widely, and at times asymmetrically, divergent (on more distant leaves on the main axis the lateral lobes often widely spreading, forming an angle of 180° with each other); branch leaves typically closely and regularly imbricate, weakly asymmetrical. Lobes narrowly attenuate, tapering from 2–4 cells wide at extreme base followed by

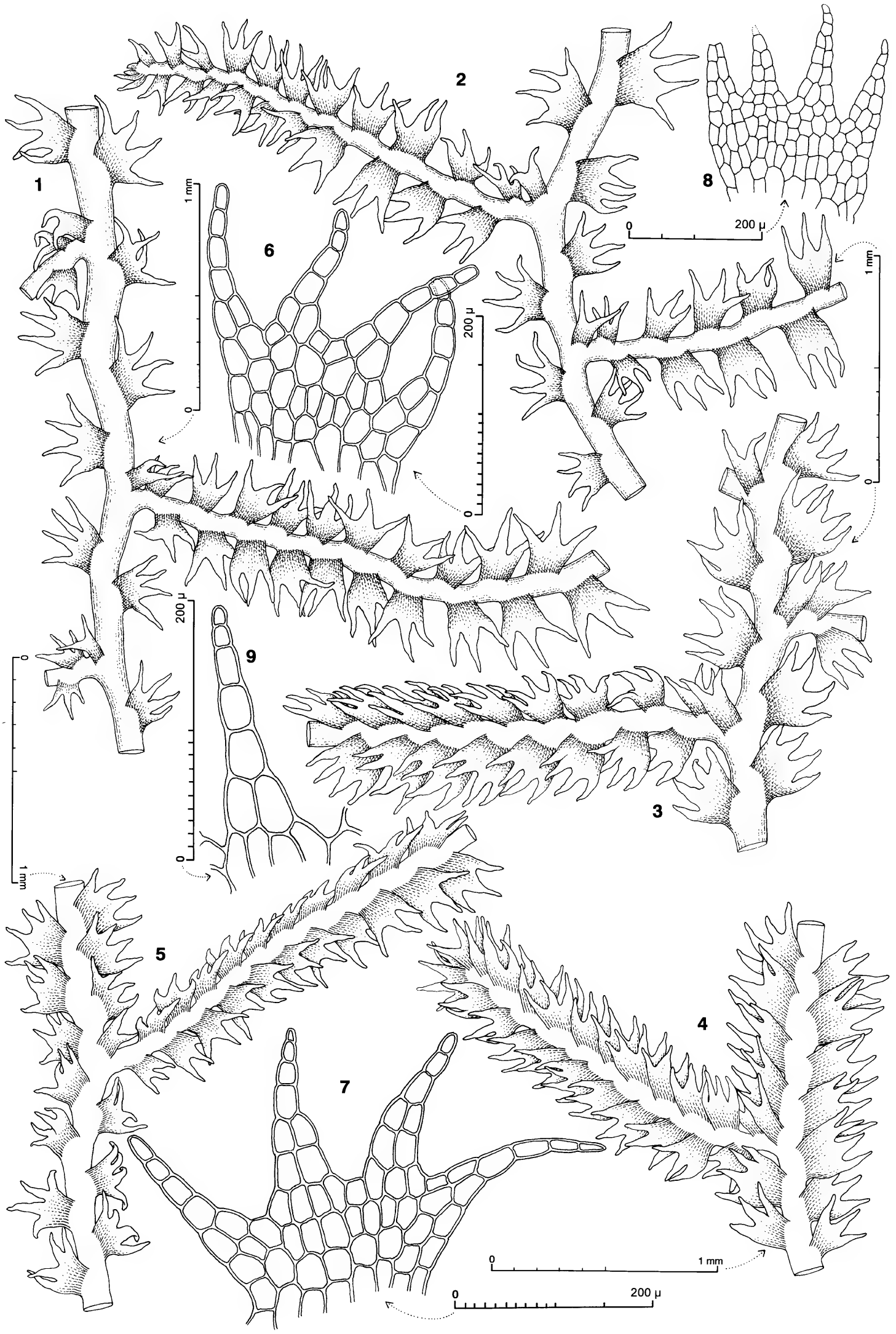

Fig. 53.
Telaranea tridactylis (Lehm. & Lindenb.) J.J.Engel & Merrill. 1–5. Portion of main shoot with 1 or more *Frullania*-type branches, dorsal view (note especially the variation in orientation and planation

1–2(4) biseriate tiers, terminating in a uniseriate row of (2)3–5 cells; cells of the uniseriate portion short to weakly elongate, moderately thick-walled. Disc ± symmetrically weakly cuneate, 3–5 cells high (disc of branch leaves to 6(7) cells high), 11–16 cells wide in distal portion narrowing to (7)8(9) cells wide in basal tier. Cells of disc typically evenly and moderately thick-walled, the areolation rather compact and lacking the regular arrangement of other *Telaranea* species (secondary divisions of disc cells random in both planes); median cells small, 18–23 μm wide × 26–38(42) μm long; basal cells considerably larger and forming an obvious tier; surface with a network of fine irregular striae. Underleaves much smaller than leaves, spreading nearly or at 90° to stem, distant, slightly convex (ventral view), 3–4-lobed to 0.45–0.55, the lobes narrowly attenuate to subciliiform, 2 cells wide at the base, terminating in a uniseriate row of 2–3 slightly elongated, somewhat thick-walled cells, or consisting entirely of the uniseriate row, terminating in a slime papilla; disc weakly cuneate, 2–3(4) cells high (median sinus), the cells in ± regular tiers; disc 9–10 cells wide in distal portion (6–8 cells wide in 3-lobed underleaves), narrowing to 8 cells wide at base (6 cells wide in 3-lobed underleaves), the basal row of cells on the whole longer and forming an obvious tier. Asexual reproduction lacking.

Dioecious. Androecia either on short *Frullania*-type branches with a few to several (to 5) cycles of normal vegetative leaves prior to androecial formation, or on short, abbreviated, ventral-intercalary branches lacking normal vegetative leaves; bracts closely imbricate, strongly dorsally assurgent, the entire bract deeply concave, 2(3)-lobed, each lobe terminating in a uniseriate row of 2–3 not to hardly elongated cells; lamina cells not tiered, irregular in shape and arrangement, the lamina margins sometimes denticulate, often with stalked or sessile slime papillae; antheridia 1 per bract, large for bract size, the stalk uniseriate; bracteolar antheridia absent. Gynoecia with bracts and bracteoles in 3 series, inserted on the vestigial perigynium; bracts becoming progressively larger and less deeply lobate toward the perianth, those of innermost series deeply concave, with apices rounded, irregularly denticulate with sporadic 1–2-celled teeth; bract margins crenulate to irregularly repand, with a few sessile slime papillae, the bracts with a border formed of 1 row of cells longer, narrower and more irregular than those within; bracteole nearly identical in size and form. Perianth 0.65–0.8 emergent, narrowly fusiform, 5–7.2× longer than wide, terete in basal half, the distal half obscurely trigonous and with 5–6 deep plicae, gradually and distinctly narrowing toward the contracted mouth; mouth with 6 narrowly triangular lobes, each lobe fringed with thick-walled, contorted, coarsely papillose cilia, the cilia consisting of 2–4 elongated cells with thickened and swollen septa, often with a knob-like swelling at the basal end of the cells just above the septa; perianth 2–4 stratose in basal portion, the median portion 2(locally 1)-stratose.

Seta with 8 rows of outer cells (each with their free face bulging), surrounding an inner core of 17–18 much smaller thin-walled cells. Capsule rather short-ellipsoidal, the wall 24–30 μm thick, of 3 layers, the outer layer subequal to the combined 2 inner layers, or slightly less thick; outer layer of cells in tiers, rather regularly short-rectangular, with two-phase development, the longitudinal walls with well-defined sheet-like thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with very few sporadic,

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of branch leaves and the imbrication of main shoot leaves). 6–8. Leaves. 9. Leaf lobe. (Figs. 1, 6, 7, 9, from type of *T. tridactylis*; 2, from *Norris 29804*, Tasmania, Arve Road; 3, from *Norris 27281*, Tasmania, above Lake Barrington near Forth Falls; 4, 8, from *Engel 19725*, Tasmania, Newhaven Road, just S of Doughboy Hill; 5, from *Norris 29470*, Tasmania, Kermandie R. at North Creek.)

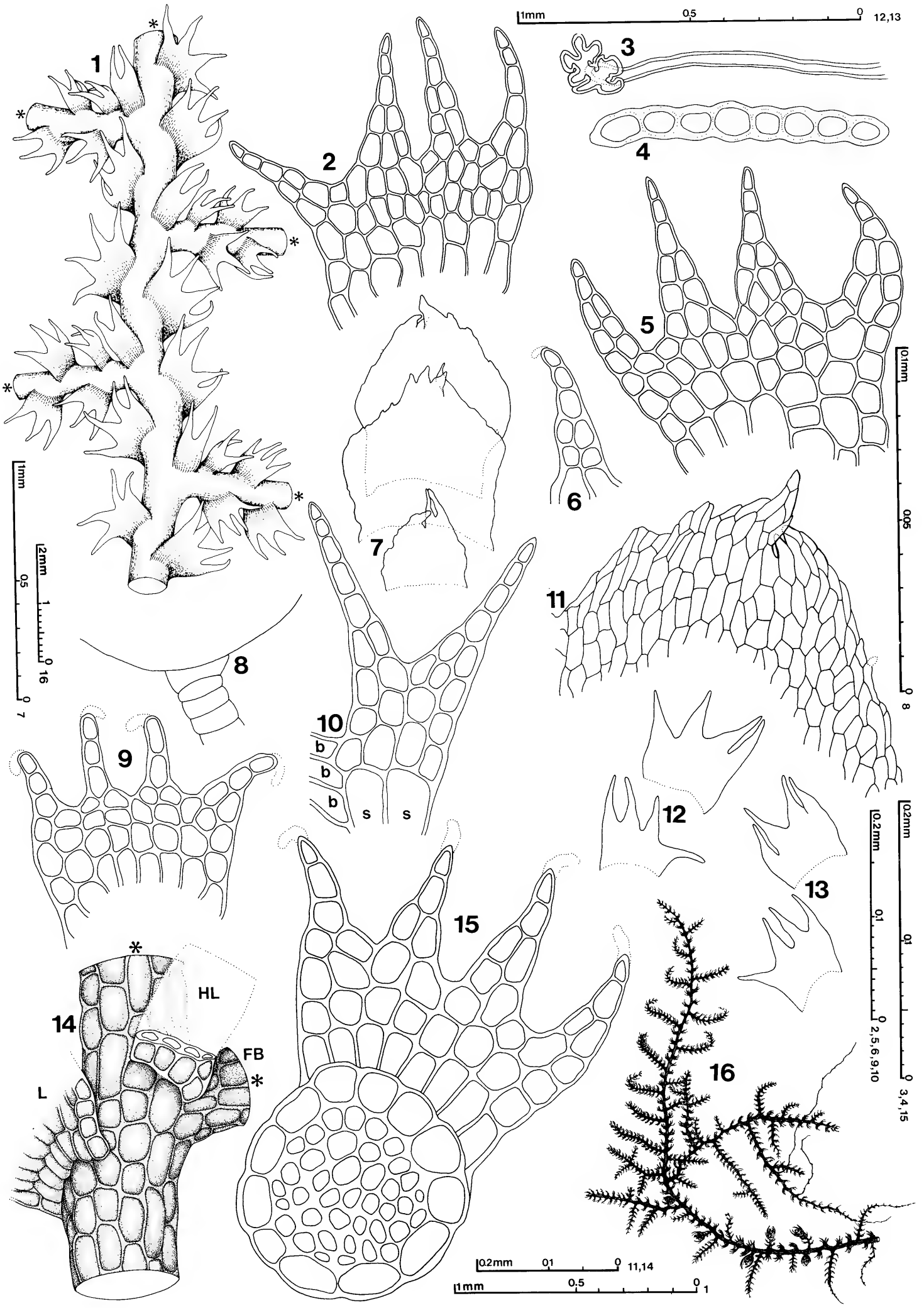

Fig. 54.
Telaranea tridactylis (Lehm. & Lindenb.) J.J.Engel & Merrill. 1. Main shoot, with 4 *Frullania*-type branches, dorsal view. 2, 5. Leaves. 3. Rhizoid with ramified tip. 4. Leaf lamina cross section. 6. First branch underleaf. 7. ♀ Bracts (top to bottom), from innermost, second and lowermost series. 8. Antheridial stalk. 9. Underleaf. 10. Half-leaf (b = adjoining branch cell; s = adjoining stem

local, non-pigmented, nodular swellings), the transverse walls devoid of thickenings; innermost layer of cells ± tiered, irregularly narrowly to broadly rectangular, with semiannular bands rather narrow, ± irregular, short or infrequently complete, rarely forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 14.9–16.8 μm in diam., the wall yellow-brown, with low, delicate papillae, coalescing to form short ridges that rarely delimit areolae. Elaters rigid, somewhat sinuous, (7.7)8.6–10.1 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–3.4 μm wide.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, South Island (sea level); Australia: Tasmania, Victoria, Queensland. In the South Island known from one station at Milford Sound (Fiordland). For remarks on reports based on misdeterminations, see Engel and Merrill (2004).

The species is primarily a forest plant throughout its range. The plant from Milford Sound occurred on exposed, moist, vertical cliffs with a dense bryophyte cover at the forest margin.

Comments: This species is the smallest member of sect. *Neolepidozia*. It is distinguished from *Telaranea patentissima* by its smaller size, smaller leaf cells (at most 25 μm wide), and less regular arrangement of disc cells, vs. cells 25–40 μm wide in *T. patentissima*, with a more *T. tetrapila*-like areolation of rather regular rows and tiers.

The branch leaves have a rather high disc (to 7 cells high) and are often 4-lobed. By contrast, the leaves of the main shoot are often distant, longitudinally inserted, and deeply divided, with widely splayed lobes, often oriented as much as 180° to each other (Fig. 53: 7; Fig. 54: 2). Weaker shoots may have both stem and branch leaves splay-lobed, and lack the flattened, ribbon-like branches (Fig. 53: 1, 2).

Sect. ***Cancellatae*** J.J.Engel & Merrill

Telaranea sect. *Cancellatae* J.J.Engel & Merrill, Phytologia 79: 250. 1996 (1995). Type: *Telaranea tetrapila* (Hook.f. & Taylor) J.J.Engel & Merrill (≡ *Lepidozia tetrapila* Hook.f. & Taylor)
Telaranea sect. *Capillares* J.J.Engel & Merrill, Phytologia 79: 251. 1996 (1995), *non Lepidozia* sect. *Capillares* Gottsche, Lindenb. & Nees, Syn. Hepat. 211. 1845. Type: *Telaranea grossiseta* (Steph.) J.J.Engel & R.M.Schust. (≡ *Lepidozia grossiseta* Steph.)

Telaranea praenitens (Lehm. & Lindenb.) E.A.Hodgs.

[Fig. 55]

Jungermannia praenitens Lehm. & Lindenb. *in* Lehm., Nov. Min. Cogn. Stirp. Pug. 6: 27. 1834. *Lepidozia praenitens* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, Syn. Hepat. 206. 1845. *Mastigophora praenitens* (Lehm. & Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III,

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cell). 11. Distal portion of innermost ♀ bract. 12, 13. Leaf outlines. 14. Portion of main shoot, dorsal view with only leaf (L) and half-leaf (HL) bases indicated (FB = *Frullania*-type branch). 15. Stem, cross section + underleaf. 16. Portion of main shoot, dorsal view, showing leaf arrangement (note 6 ♂ branches toward base). (All from *Norris 29470*, Tasmania, Kermandie R.)

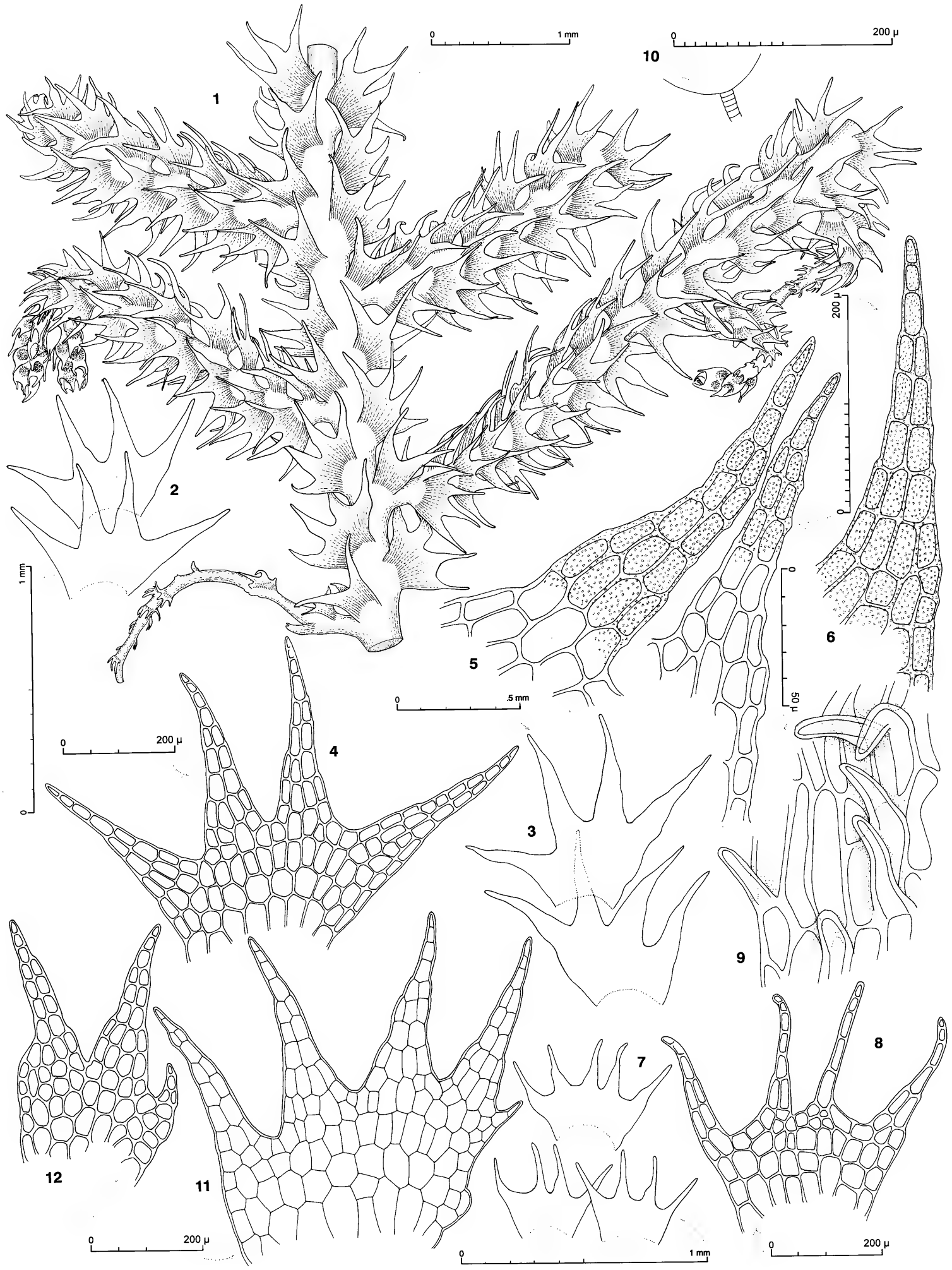

Fig. 55.
Telaranea praenitens (Lehm. & Lindenb.) E.A.Hodgs. (figs. 1–10, var. *praenitens*; 11, 12, var. *dentifolia*). 1. Sector of main shoot showing androecia on primary and secondary terminal branches, dorsal view. 2, 3. Leaves (note symmetry). 4. Leaf, cellular detail. 5, 6. Dorsal lobes of leaves. 7. Underleaves. 8. Underleaf, cellular detail. 9. Sector of perianth surface immediately below mouth. 10. Antheridial stalk. 11. Leaf. 12. Half-leaf. (Figs. 1, 2, 4, 6–8, 10, from *Engel 18935*, New Zealand, South Is., Westland EP, near Waiho R. between Wombat Terrace and Cana-

4: 416. 1877. *Telaranea praenitens* (Lehm. & Lindenb.) E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. Type: New Zealand, South Is., Dusky Bay, *Menzies* (G!, S! [3 seen]).

Plants with a rather spiny appearance, soft, flexuous yet firm, loosely prostrate, often in dense, compact mats, dirty yellowish green, nitid when dry; shoots small to medium, to 0.9 cm wide, including branches. Branching mostly regular and loosely to less often quite densely 1-pinnate, the branches remaining rather short, normally determinate, not much differing in length (rather than plumose), the branches of the *Frullania* type; branch half-leaf bilobed, narrowly rectangular to cuneate (then with lobes diverging), entire (or with one or both margins toothed in var. *dentifolia*); first branch underleaf undivided and ciliiform, inserted on ventral side of branch near juncture of branch and main axis. Ventral-intercalary branches occasional, often becoming leading shoots and leafy throughout. Stems with cortical cells markedly differentiated, the radial walls thin, the outer wall somewhat thickened, in 12–13 rows, those on ventral side of stem a little smaller; cortical cells in section larger than the numerous (ca. 50–65) medullary cells. Rhizoids not seen. Leaves on main shoot rigid, at least the disc widely spreading, distant to loosely imbricate, plane to moderately concave, the lobes somewhat incurved, the insertion moderately to distinctly incubous; leaves 510–870 μm wide × 455–595 μm long, moderately to distinctly asymmetric (the dorsal lobes paired), ± equally and rather deeply palmately 4-lobed to ca. 0.5–0.65 (very rarely [1 population] 5–6-lobed), the lobes subequal to somewhat longer than the disc in length. Lobes attenuate, 4 cells wide for 1–3 tiers at extreme base (5–6 cells wide at base in var. *dentifolia*), biseriate for much of their length, terminating in a short uniseriate row of 2–4(5) cells (typically less than half the length of lobe), the lobe margins contracted at the transition from 4 cells wide to 2 and from 2 cells wide to 1; lobe cells ± firm, moderately thick-walled, the septa thickened in the corners and swollen and projecting from the lobe margins, the lobe cells rectangular and not narrowing distally; surface finely to distinctly striate-papillose. Disc somewhat asymmetrically short-cuneate, 4–5 cells high (from median sinus base to leaf base), 15–16(19) cells wide in distal portion narrowing to 8–10 cells wide in basal portion; margins entire (sporadically toothed in var. *dentifolia*), the dorsal margin often bluntly denticulate by projecting septa at the ends of cells, ± straight. Cells of disc moderately thick-walled, trigones minute to small, the median disc cells 22–38 μm wide × (38)43–60 μm long, in ± regular tiers or somewhat irregularly arranged; basal 1–2 rows of disc cells larger; surface smooth or faintly striate-papillose distally. Underleaves much smaller than leaves, strongly spreading to subsquarrose, distant, plane, 4(rarely 5)-lobed to ca. 0.5, the lobes ciliiform, straight, 2–3 cells wide at the base, the uniseriate portion formed of 3–4(5) elongated, ± thick-walled cells with thickened septa, often terminating in a slime papilla; disc symmetrically cuneate, 3–4(5) cells high (median sinus), the cells in irregular tiers, the disc 11–17 cells wide in distal portion narrowing to 8–9(12) cells wide at base; margins entire, usually straight.

Plants dioecious. Androecia either terminal on short to moderately long primary or secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary, spicate branches; bracts closely imbricate, strongly dorsally assurgent, deeply concave, bilobed to ca. 0.4, the lobes acuminate, terminating in a uniseriate row of 2–4 not to slightly elongated cells; dorsal margin of lamina irregularly crenulate, with a few stalked or sessile slime papillae; bracts monandrous; antheridia large for bract size, the stalk uniseriate; bracteolar antheridia absent. Gynoecia with bracts small for perianth size, those of innermost series concave, broadly ovate to

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vans Knob; 3, 5, from *Engel 6667B*, New Zealand, South Is., Westland EP, Lake Wombat; 9, from *Reif C63B*, New Zealand, South Is., Westland EP, Camp Creek; 11, 12, from type of var. *dentifolia*.)

suborbicular, ± regularly 3–4-lobulate, the lobules terminating in a pair of laterally juxtaposed cells or a single cell; lamina composed of ± regularly subrectangular cells, the margin bordered by cells of variable shape, often long and narrow, the apical or free end of marginal cells often divergent and forming a crenulation, the margins thus irregularly crenulate, otherwise with a sporadic unicellular tooth and a few slime papillae; bracteoles of innermost series similar in form and size to bracts. Perianth long-emergent, fusiform, terete in basal and median sectors, the distal sector obscurely trigonous and with 4–5 plicae, the perianth narrowing toward the strongly contracted mouth; mouth cells thick-walled, often sinuate, partially or wholly laterally free, occasionally with a laterally free uniseriate row of 2 cells, the mouth thus denticulate-subciliate, the surface cells immediately below mouth often with their apical end projecting as a blunt, thick-walled tooth; perianth 2–3-stratose in basal portion, the median portion 2-stratose.

Seta with 8 rows of outer cells (each with their free face bulging), surrounding an inner core of 19–20 much smaller cells. Capsule rather long-ellipsoidal, 420–560 μm wide × 980–1260 μm long, the wall 26–34 μm thick, of 3 layers, the outer layer subequal to or slightly less thick than the combined 2 inner layers; outer layer of cells in tiers, rather regularly short-rectangular, with two-phase development, the longitudinal walls with well-defined sheet-like thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, local, non-pigmented, nodular swellings), the transverse walls devoid of thickenings; innermost layer of cells ± tiered, irregularly narrowly to broadly rectangular, with semiannular bands common, rather narrow, close, usually complete, at times forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 12–13 μm in diam., the wall yellow-brown, areolate (with a low, delicate, close network of furcate ridges that coalesce and delimit areolae). Elaters rigid, nontortuous, 9.6–12 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.4–3.8 μm wide.

Comments: *Telaranea praenitens* has been widely misunderstood. It is, however, one of the easiest of our species to recognize, marked by the rather deeply palmately lobed leaves (to 0.6), and the minute denticulations formed by the swollen projecting septa on the lobes and disc margins (Fig. 55: 5, 6). In addition, the surface of the lobes is almost always distinctly papillose (Fig. 55: 5, 6).

A noteworthy feature of this species is the scabrous condition of the perianth surface. The cells immediately below the mouth are prorate, their apical ends projecting as blunt, thick-walled teeth (Fig. 55: 9).

Two varieties are recognized for the species, as follows.

Key to Varieties

1a. Margins of leaves and half-leaves devoid of teeth; leaf lobes 4 cells wide at base, the cells in basal portion of lobe elongate (ca. 2:1). Throughout New Zealand . . . . . var. *praenitens* (p. 289)

1b. Margins of leaves and half-leaves (and rarely the lobes) sporadically with 1(2) multicellular teeth; leaf lobes (at least the median) often 5–6 cells wide at base, the cells of lobe bases somewhat shorter, at times ± isodiametric. Local, southern half of South Is. . . . . var. *dentifolia* (p. 289)

Telaranea praenitens (Lehm. & Lindenb.) E.A.Hodgs. var. ***praenitens***

Lepidozia beckettiana Steph., Sp. Hepat. 3: 593. 1909. Lectotype (*fide* Engel and Merrill, 2004): New Zealand, South Is., Westland, Kellys Ra., 30 Jan. 1903, *Beckett "4310" – c. per.* (G!). Isolectotype: (*Beckett 363*, CHR 585842 ex herb. Beckett!).

Leaf and half-leaf margins devoid of teeth; leaf lobes 4 cells wide at base, the cells in basal portion of lobe elongate (ca. 2:1); margins of disc and lobe typically minutely denticulate by protruding end walls of the marginal cells.

Distribution and Ecology: Endemic to New Zealand: Stewart Island, South Island (10–670[1520] m), North Island (610–1320 m); for comments on extraterritorial records see Engel and Merrill (2004). Known from Fiordland, Westland, Canterbury (near Main Divide), Western Nelson, Southern North Island, Volcanic Plateau, Taranaki and Gisborne EPs.

A rather widespread species on South and North islands, occurring in wet, rich lower- to upper-elevation forests, where often on rotted logs, particularly when largely bryophyte-covered. It occurs, for example, in rich, mixed *Nothofagus* forests with a tree-fern understory (Tutoko River, Fiordland); in *Prumnopitys taxifolia – Podocarpus* flood-plain forests (Waiho River area, Westland); in *Nothofagus menziesii – Dacrydium cupressinum – Podocarpus* forests along the Tiropahi River (Western Nelson); and in *N. menziesii – Raukawa simplex – Podocarpus totara – Dracophyllum* forests (Panekiri Ra., Urewera Natl. Park). It only sporadically inhabits soil or humus of the forest floor, or moist banks, etc.

The species is rarely penalpine. It was recently found at 1520 m on Mt. Arthur (Western Nelson) in communities of penalpine cushion vegetation, rocky herbfields, and *Dracophyllum*, where it occurred over decaying blades at the base of a grass immediately adjacent to a small, stagnant pool.

Telaranea praenitens var. ***dentifolia*** J.J.Engel & Merrill

Telaranea praenitens var. *dentifolia* J.J.Engel & Merrill, Phytologia 79: 253. June 1996 (1995). Holotype: New Zealand, South Is., Fiordland, Dusky Sound, Supper Cove, 11 Feb. 1946, *Allan*, as *Lepidozia gottscheana* (CHR); isotype: (F).

Leaves, half-leaves, and rarely lobes with disc margins sporadically armed with 1(2) multicellular teeth; leaf lobes (at least the median) often 5–6 cells wide at base; cells of lobe bases at times ± isodiametric; end walls of marginal cells of disc and lobes often indistinctly or not swollen and protruding.

Distribution and Ecology: Endemic to New Zealand: South Island (15–250 m). Known only from Fiordland and Westland (Lake Paringa) EPs.

Known from a limited number of collections, all from the wet, southwestern sector of South Island. The type occurred intimately intermixed with *Riccardia* sp., and the Lake Paringa collection is mixed with *Rhaphidorrhynchium amoenum*. The variety appears to be a lowland forest plant.

Comments: This variety and the typical expression of the species both have rather deeply divided, palmately lobed leaves which distinguish *Telaranea praenitens* from other members of the sect. *Neolepidozia*, although the septa between cells are not so distinctly swollen and protruding as in var. *praenitens*. The combination of rather broad leaf lobes, marginal teeth

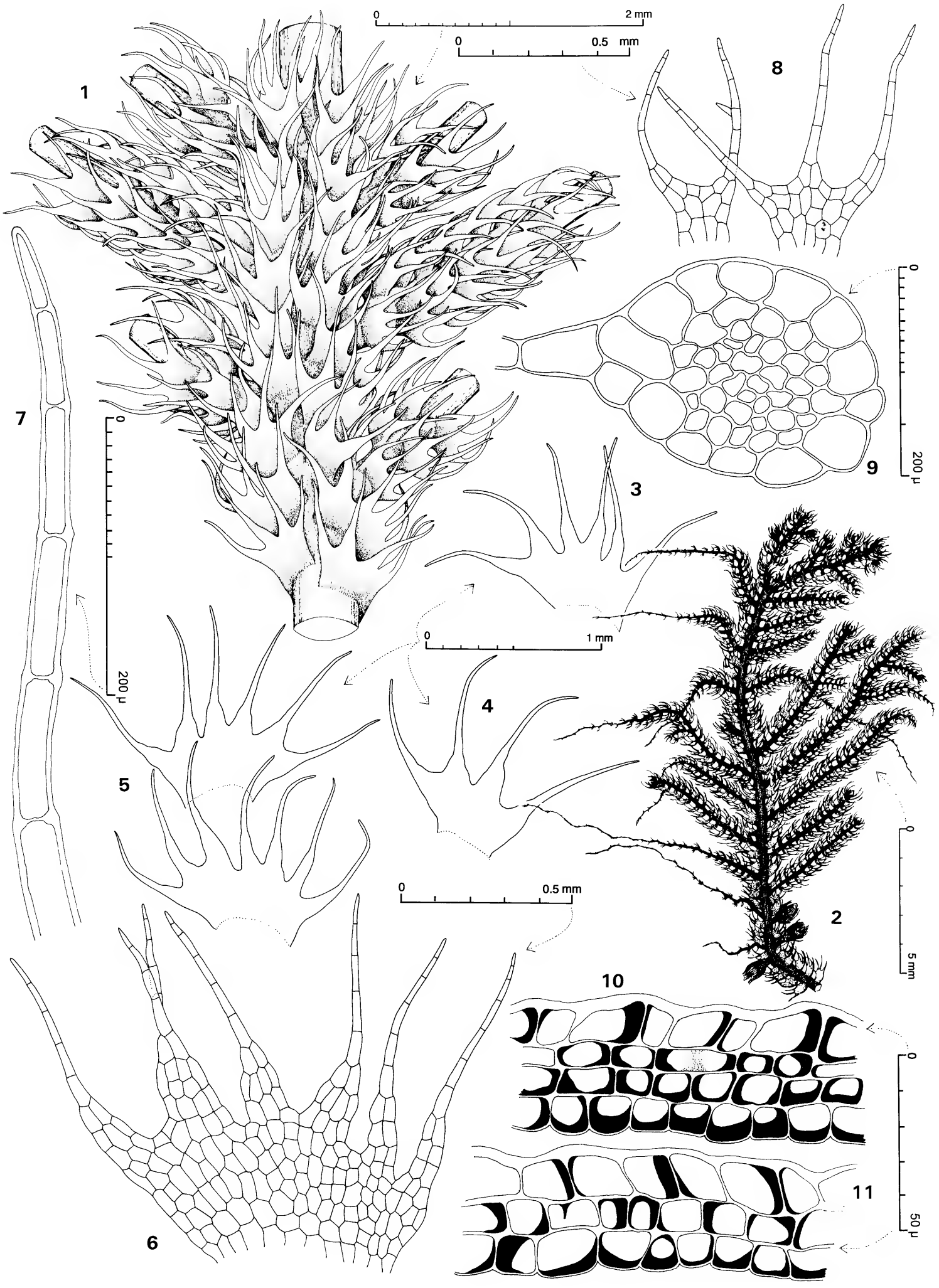

Fig. 56.
Telaranea gibbsiana (Steph.) E.A.Hodgs. 1. Shoot with 6 *Frullania*-type branches, dorsal view (note 2-, 3- and 4-lobed half-leaves). 2. Shoot with 3 young gynoecia toward base, dorsal view. 3–6. Leaves. 7. Distal portion of leaf lobe. 8. First branch underleaves. 9. Stem, cross section. 10, 11. Capsule wall cross sections. (Figs. 1–9, from *Hodgson s.n.*, New Zealand, North Is., Gisborne EP, Lake Waikaremoana [F]; 10, 11, from *Engel 20513*, New Zealand, North Is., Gisborne EP, Urewera Natl. Park, Waikareiti Track.)

(Fig. 55: 11) and papillose surface are reminiscent of *Temnoma* spp.; the well-developed stem hyaloderm, however, marks this plant as a *Telaranea*.

Telaranea gibbsiana (Steph.) E.A.Hodgs.

[Plate 6D; Fig. 50: 5, oil-bodies, p. 268; Figs. 56, 57]

Lepidozia gibbsiana Steph., Sp. Hepat. 6: 328. 1922. *Telaranea gibbsiana* (Steph.) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 70. 1965. Type: New Zealand, North Is., without specific loc., *Gibbs 1041* (G!).

Plants subisophyllous, soft, with a hairy appearance, flexuous yet firm, prostrate to ascending, in dense, compact mats, pale green (to deep olive-green in herb.), highly nitid when dry; plants medium, to 0.8 cm wide, including branches. Branching regularly rather densely and closely 1-pinnate, occasionally locally 2- or 3-pinnate, nearly exclusively of the *Frullania* type; branch half-leaf 2–4-lobed, cuneate (the lobes diverging, even when bifid); first branch underleaf undivided and ciliiform or 2(3)-fid, inserted on ventral or less often ventral-lateral side of branch near or at juncture of branch and main axis. Ventral-intercalary branches occasional, often becoming leading shoots and leafy throughout. Stems with cortical cells distinctly differentiated, thin-walled, in 13–15 rows; cortical cells in section much larger than the numerous (34–47) medullary cells. Rhizoids observed only on stoloniform axes. Leaves on main shoot rigid, suberect to widely spreading, loosely to closely imbricate, concave reflecting the incurving of lobes, the insertion moderately to distinctly incubous; leaves 720–1275 μm wide × 600–890 μm long, subsymmetric to less often asymmetric, 4–6(7)-lobed to (0.6)0.65–0.75, the lobes longer than the disc. Lobes ciliiform, rigid, the base subtriangular, (3)4(5) cells wide at extreme base, terminating in a uniseriate row of 5–7(8) cells; cells of the uniseriate portion ± thick-walled, the septa thickened in the corners and swollen. Disc ± symmetrically cuneate, 4–6 cells high (from median sinus base to leaf base), 15–22 cells wide in distal portion narrowing to 8–15 cells wide in basal portion. Cells of disc thin-walled but not delicate, trigones minute to small, the median cells large, 36–65 μm wide × 50–72(78) μm long; basal 1–2 rows of disc cells considerably larger (wider and on the whole a little longer), often not in regular tiers; surface with network of fine, irregular, elongate striae. Oil-bodies in all leaf cells, including all cells of cilia, hyaline, 7–9 per median disc cell, finely botryoidal, broad to narrowly elliptic to fusiform, spherical and 4–7 μm in diam. or ellipsoidal to ovoid and 4–7 × 4–13 μm. Underleaves somewhat smaller than leaves, strongly spreading to subsquarrose, contiguous to loosely imbricate, plane, 4–6(8)-lobed to 0.6–0.8, the lobes ± symmetrically divergent, ciliiform, straight to arched, the uniseriate portion formed of 5–7(8) elongated, ± thick-walled cells with swollen septa, not terminating in a slime papilla; disc symmetrically cuneate, 3–4(5) cells high (median sinus), the cells often not in regular tiers, the disc 9–17 cells wide in distal portion narrowing to (8)10–12 cells wide at base. Asexual reproduction lacking.

Plants dioecious. Androecia on short, abbreviated, ventral-intercalary, spicate branches from main shoot or primary, *Frullania*-type branches; bracts closely imbricate, strongly dorsally assurgent, ± cucullate, bilobed to ca. 0.3, the lobes acuminate, terminating in a uniseriate row of 2–3(4) cells, the basal cell isodiametric to rather elongated, the terminal cell ± thick-walled, often curved, rather elongated, to 3.5:1; dorsal margin of lamina somewhat dilated and incurved, entire, bordered by 1–2 rows of elongated, very thin-walled cells, without slime papillae; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent.

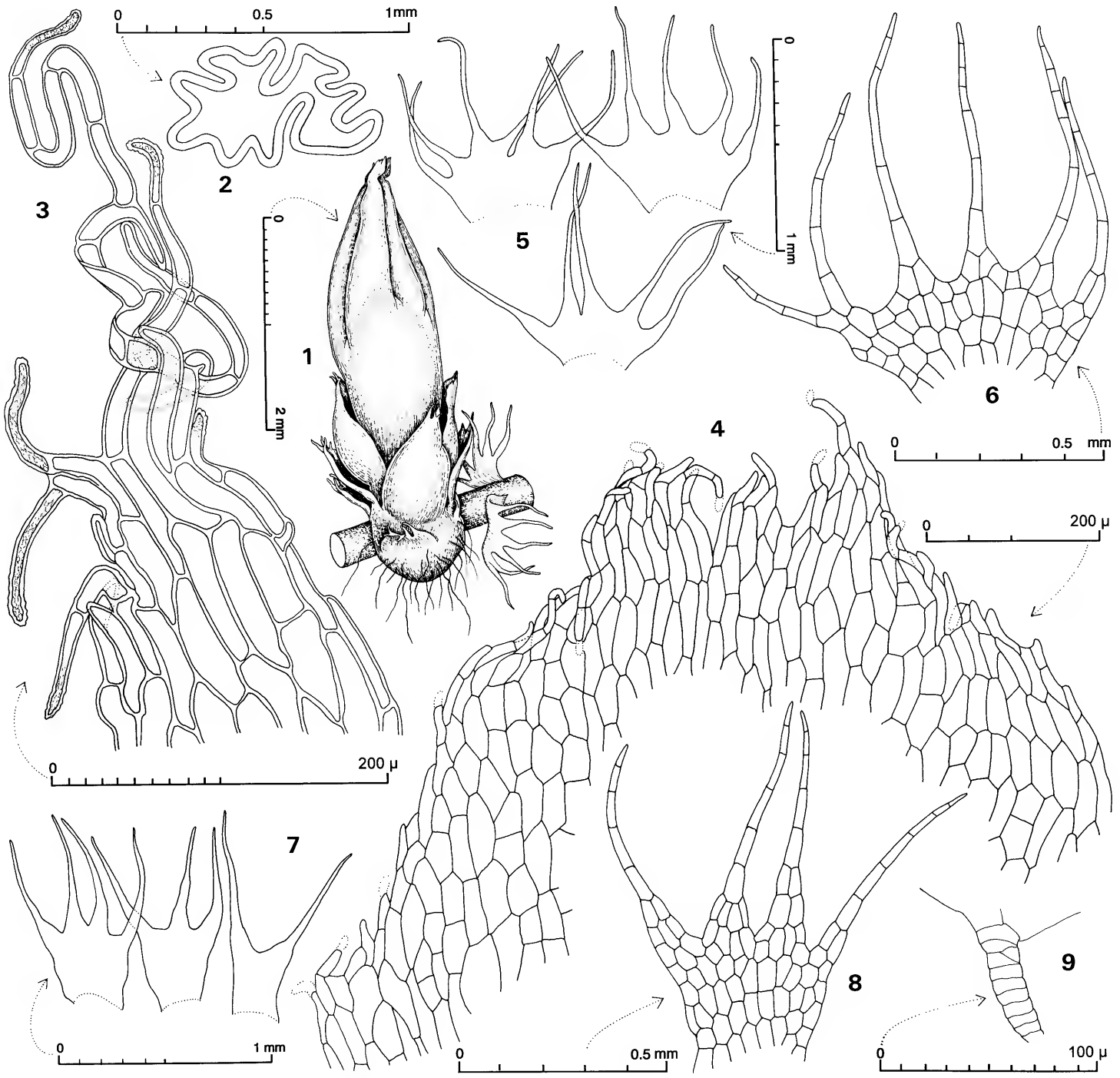

Fig. 57.
Telaranea gibbsiana (Steph.) E.A.Hodgs. 1. Gynoecium. 2. Cross section through distal portion of perianth. 3. Portion of perianth mouth. 4. Distal portion of innermost bract. 5. Underleaves of main shoot. 6. Underleaf. 7. Half-leaves. 8. Four-lobed half-leaf. 9. Antheridium. (Figs. 1–8, from *Hodgson s.n.*, New Zealand, North Is., Gisborne EP, Lake Waikaremoana [F]; 9, from *Hatcher 1301*, same loc.)

Gynoecia with bracts becoming progressively larger and less deeply lobate toward the perianth, those of innermost series ensheathing the perianth, deeply concave, the apical portion canaliculate, the bracts ± suborbicular, with apices irregularly 4-lobulate, the lobules terminating in a uniseriate row of 1–2 cells; bract margins crenate to dentate, the armature frequently sharply inflexed, often terminating in a slime papilla, the bracts with an obscure border formed of 1 to several rows of cells longer, narrower and more irregular than those within; bracteoles nearly identical in form to bracts although a little smaller. Perianth 0.5–0.55 emergent, ovoid-cylindrical, terete in basal half, the distal half obscurely trigonous and with 6–9 plicae, the sulci shallow to deep; perianth narrowed toward a decidedly contracted mouth, the mouth with 6 narrowly triangular lobes, each lobe fringed with slightly thick-walled, contorted, crowded, sparingly papillose cilia, the terminal cell of each cilium coarsely papillose.

Seta seen only in collapsed state. Capsule wall 32–40 µm thick, of 3–4 layers, the outer layer

subequal to 2 of inner layers; outer layer of cells weakly tiered, rather regularly short-rectangular, with two-phase development, the longitudinal walls with well-defined sheet-like thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with occasional local, not or weakly pigmented, nodular swellings), the transverse walls devoid of thickenings or with 1–2 nodular swellings; innermost layer of cells in weakly defined tiers, irregularly narrowly rectangular; semiannular bands common, rather wide, close, usually complete, at times forked and anastomosing to delimit ill-defined, local fenestrae.

Spores and elaters not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (80–740 m), North Island (305–1320 m). Known from Western Nelson, Taranaki, Gisborne and Northland EPs.

The species appears to be locally and sporadically distributed in the North Island. It occurs in forests of *Weinmannia racemosa*, *Nothofagus fusca* and mixtures of these two species, but has also been found under *Lagarostrobos colensoi – Lepidothamnus intermedius* forest (Mt. Burnett, Western Nelson). Known from several sites in the Lake Waikaremoana area (Urewera Natl. Park); there it occurs on ground, soil banks, exposed roots, rotted stumps and bryophyte-covered logs, etc., in forests between 540 and 1320 m (where recorded). It is also locally abundant in the Waipoua *Agathis australis* forests, where it is associated with *Hymenophyllum*, *Dicranoloma* and *Trichocolea* over rotten logs. The plant is known from several South Island localities, all in Western Nelson, with a southern limit in the Brunner Ra., occurring abundantly on humus in a *Podocarpus – N. fusca* forest. It has been found with *Bazzania adnexa*, *Chiloscyphus echinellus*, *Heteroscyphus billardierei*, *Hymenophyllum demissum*, *Kurzia hippuroides*, *Lepicolea scolopendra*, *Lepidozia kirkii*, *Leptoscyphus australis*, *Rhizogonium distichum*, *R. pennatum*, *Telaranea herzogii*, *Wijkia extenuata*, *Zoopsis argentea* var. *flagelliformis* and *Z. setulosa*.

Comments: *Telaranea gibbsiana* is one of our largest *Telaranea* species and is most closely allied to *T. grossiseta* of Tasmania. Both are relatively robust plants (for the genus), with a high disc, ciliiform leaf lobes, and the cells of the uniseriate row distinctly elongated and capillary. The septa are thickened in the corners and swollen and projecting (Fig. 56: 7). Similar projecting septa occur in *T. praenitens*.

Telaranea hodgsoniae J.J.Engel & Merrill

[Fig. 58]

Telaranea hodgsoniae J.J.Engel & Merrill, Phytologia 79: 251. June 1996 (1995). Holotype: New Zealand, South Is., Canterbury Prov., Peel Forest, ca. 1500 ft., *Child H2084 – c.* ♂ (F); isotype: (CHR).

Plants rather stiff and firm, prostrate, in compact mats, glaucescent, whitish green, the surface rather dull and water-repellent, subnitid when dry; plants ± stenotypic in stature, small, to 0.6 cm wide, including branches. Branching irregularly to rather regularly 1-pinnate, the branches of the *Frullania* type, short; branch half-leaf 2-lobed, linear-rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided, subulate, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches sporadic, leafy, becoming leading shoots. Stems with cortical cells distinctly differentiated, thin-walled, in 13 rows; cortical cells in section much larger than the numerous (ca. 52) medullary cells. Leaves on main shoot rigid, obliquely spreading, rather closely imbricate, moderately convex

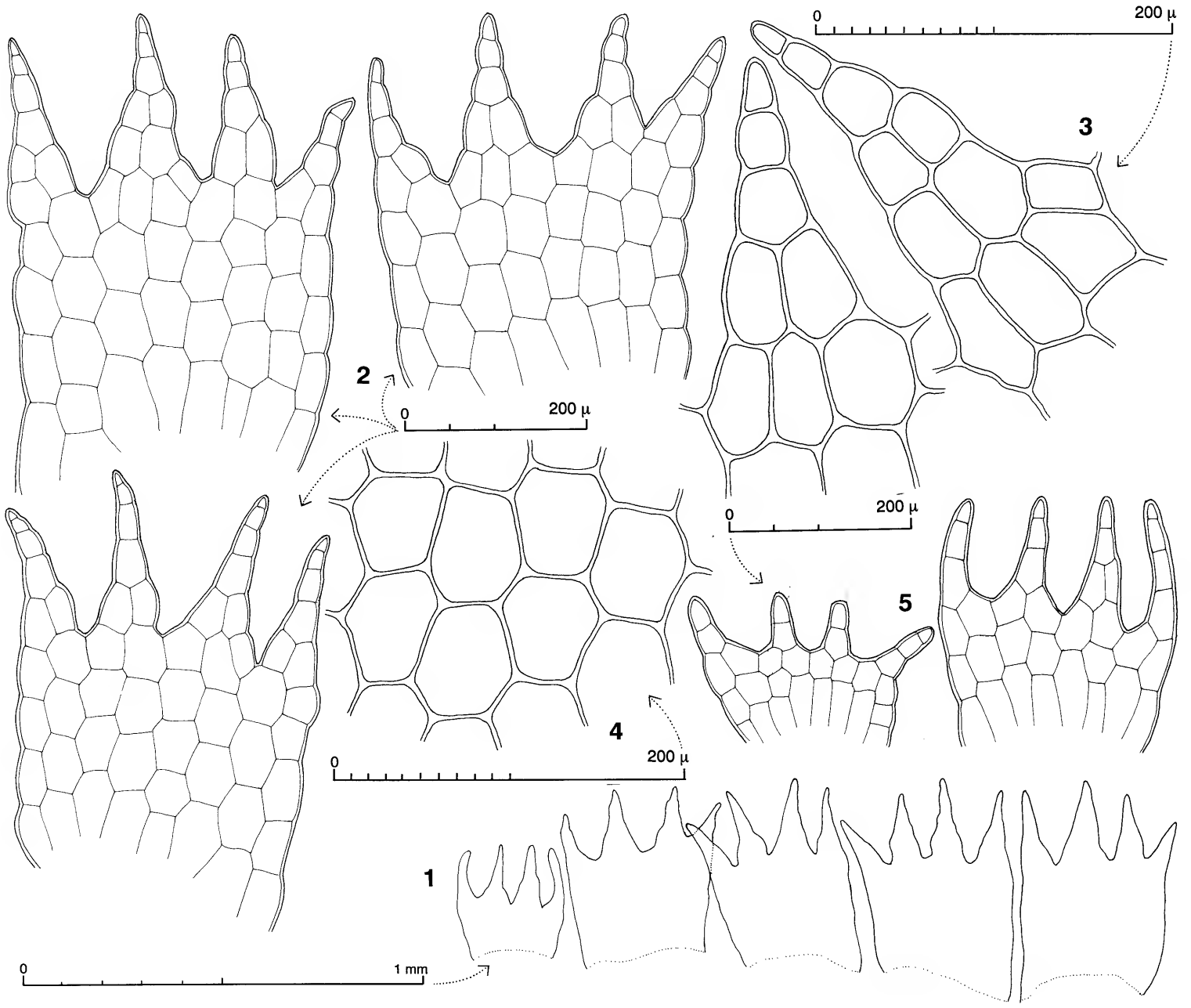

Fig. 58.
Telaranea hodgsoniae J.J.Engel & Merrill. 1. Leaves and to left, an underleaf. 2. Three leaves, cellular detail. 3. Median leaf lobes. 4. Median disc cells. 5. Underleaves, cellular detail, stippled walls indicate formation of rhizoid initials. (All from holotype.)

(especially when dry), the insertion distinctly incubous; leaves 315–350(420) µm wide × 350–525 µm long, subsymmetric, (3)4-lobed to 0.4–0.5, the lobes much shorter than the disc. Lobes narrowly acute, 2–3(4) cells wide at extreme base, terminating in a short uniseriate row of 2–3 cells; lobe cells short, ± isodiametric to short-rectangular, bulging, moderately thick-walled, the cell walls weakly thickened in the corners but the septa not swollen and projecting; surface as in disc. Disc symmetric, subquadrate, 4–5 cells high (from median sinus base to leaf base), 8(9) cells wide in both distal and basal portion; cells of margins often bulging. Cells of disc evenly and moderately thick-walled and firm, trigones minute, the cells ± isodiametric, those in median sector 38–50(55) µm wide × 43–62(70) µm long, the cells in ± regular longitudinal rows, but somewhat offset transversely; surface with a hazy, granular appearance. Underleaves much smaller than leaves, ca. 1.3× stem width, patent to strongly spreading, distant, plane, 4-lobed to 0.5–0.6, the lobes straight, consisting of a uniseriate row of 3(4) short cells (the lobes 2 cells wide at extreme base) terminating in a slime papilla; disc subquadrate to weakly cuneate, 3 cells high (median sinus), the cells ± regularly arranged, the disc 8 cells wide, the cells in distal tier sporadically secondarily divided to form rhizoid initials; margins entire, usually straight.

Asexual reproduction lacking.

Plants apparently dioecious. Androecia on short, abbreviated, ventral-intercalary branches from leading shoots or from flagelliform branches; bracts closely imbricate, dorsally assurgent, deeply concave, 2-lobed, each lobe terminating in a single cell or a uniseriate row of 2–3 not to hardly elongated cells; lamina cells irregular in shape and arrangement, the dorsal lamina margin feebly dilated, feebly and irregularly crenulate, no slime papillae seen; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands, South Island (30–1390 m), North Island (850 m). Known from Otago (Dunedin), Westland (Nelson Lakes Natl. Park) and Southern North Island (Wellington, Tararua Ra.) EPs.

In the South Island known only from scattered sites and in the North Island only from the extreme southern sector (Tararua Ra.). It is apparently a forest species and may cover many square meters on steep, shaded, silty, damp banks in, for example, *Leptospermum scoparium* or *Melicytus ramiflorus* forest (Otago) or *Nothofagus fusca – N. solandri* forest (Nelson Lakes Natl. Park).

Comments: The plant resembles a diminutive *Telaranea tetrapila*. The parallel-sided leaf disc (Fig. 58: 1, 2) is reminiscent of the var. *roseana* of that species, being only 8 cells wide throughout, although only 4–5 cells high (Fig. 58: 2). However, the cells appear small and firm-walled, and the lobes are rather stout and stubby, and not attenuate. The plants are rather uniform in size, small and not more than 0.6 cm wide, including the branches.

Plants of *Telaranea hodgsoniae* often appear somewhat dull under the dissecting microscope, but are never glaucous as in *T. tuberifera*. Under the compound microscope, the cells have a hazy, granular appearance, rather like frosted glass.

Telaranea patentissima (Hook.f. & Taylor) E.A.Hodgs.

[Figs. 59, 60]

Jungermannia patentissima Hook.f. & Taylor, London J. Bot. 3: 386. 1844, (3: 286 [*sic*] *in errore pro* 386). *Lepidozia patentissima* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 204. 1845. *Mastigophora patentissima* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Telaranea patentissima* (Hook.f. & Taylor) E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. Type: Auckland Is., *Hooker* (BM! [4 seen], FH!).

Plants soft, often spinescent, flexuous yet firm, prostrate, in loose to compact mats, pale green to yellowish green, nitid when dry; plants rather stenotypic in stature, small, to 0.8 cm wide, including branches. Branching irregularly to somewhat regularly 1-pinnate, never 2-pinnate, the branches of the *Frullania* type; branch half-leaf bifid, narrowly rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided and ciliiform to subulate, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional to common, leafy, often becoming leading shoots. Stems with cortical cells distinctly differentiated, thin-walled, in 11–12 rows, the outer walls somewhat thicker; cortical cells in section larger than the numerous (ca. 25–45) medullary cells. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rigid, obliquely spreading, distant (especially in small phases) to imbricate, plane to moderately convex, noticeably narrowing to the base, the insertion typically distinctly incubous; leaves 335–545 μm wide × 345–580 μm long, subsymmetric to moderately asymmetric, 4(6)-lobed to 0.4–0.5, the lobes about equal to or shorter

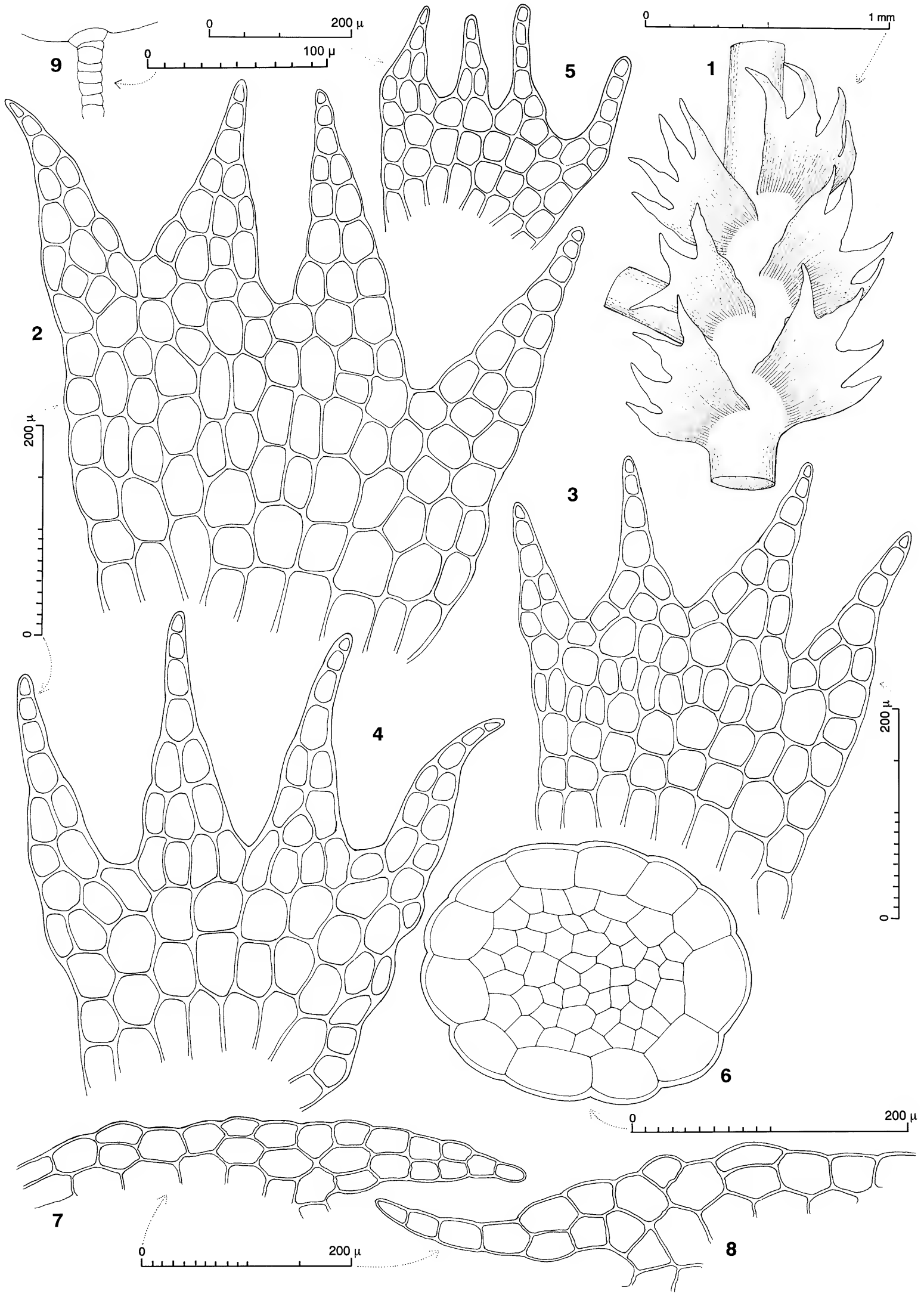

Fig. 59.
Telaranea patentissima (Hook.f. & Taylor) E.A.Hodgs. (figs. 3–5, 9, var. *patentissima*; 1, 2, 6–8, var. *ampliata*). 1. Sector of main shoot, dorsal view. 2–4. Leaves, cellular detail. 5. Underleaf, cel-

than the disc. Lobes narrowly acute to attenuate, 2–4(5) cells wide at extreme base, the two median lobes typically somewhat larger (and at times 3–4 cells wide in basal sector), often biseriate for 1–2(3) tiers, terminating in a uniseriate row of 2–4(5) cells, typically less than half the length of lobe (except var. *zebrina*); lobe cells short, ± isodiametric to short-rectangular, thin- to moderately thick-walled, the septa somewhat thickened in the corners but not swollen and projecting; surface smooth to finely striate-papillose (at least the distal half of lobes). Disc symmetrically to somewhat irregularly cuneate, 4–5 cells high from median sinus base to leaf base (up to 6[7] cells high in var. *ampliata*), 10–15 cells wide in distal portion (8 cells wide in smaller leaves) narrowing to (5)8(12) cells wide in basal portion; cells of disc and lobe margins often bulging. Cells of disc thin- to moderately and evenly thick-walled and firm, with small but distinct trigones, the cells in median sector of disc subquadrate to somewhat elongate, 25–42 μm wide × 38–55 μm long; surface smooth (coarsely striolate-papillose in var. *zebrina*). Underleaves somewhat to much smaller than leaves, variable in size, ca. 1–1.5× stem width, strongly spreading, distant to less often contiguous, plane, (3)4-lobed to 0.35–0.45, the lobes biseriate at base (except var. *zebrina*), with a uniseriate row of 2–4 rather short cells, terminating in a slime papilla; disc symmetrically subquadrate to weakly cuneate, 3–4 cells high (median sinus), (8)10–14 cells wide in distal portion narrowing to 8 cells wide at base (8 cells wide throughout in var. *zebrina*). Asexual reproduction lacking.

Plants dioecious. Androecia mostly on short, abbreviated, ventral-intercalary, spicate branches from main shoot or, occasionally, from primary, flagelliform *Frullania*-type branches; bracts closely imbricate, dorsally assurgent, deeply concave, bilobed to ca. 0.35, the lobes short-acuminate, terminating in a uniseriate row of 2(3) cells, the basal cell slightly longer than wide, the terminal cell to ca. 2:1; dorsal margin of lamina somewhat dilated, crenulate, with a few slime papillae; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent. Gynoecia with bracts small for perianth size, those of innermost series concave, oblong to suborbicular, very shallowly and irregularly 3–4-lobulate, the lobules terminating in single curved cell or several sinuous, laterally juxtaposed cells, sometimes irregularly denticulate; lamina composed of ± regularly subrectangular cells, the margin bordered by narrower elongated cells, the apical or free end of marginal cells often divergent and forming a blunt tooth, especially distally, the margins otherwise with a sporadic unicellular tooth and a few slime papillae; bracteoles smaller but similar in form to bracts. Perianth long-emergent, fusiform, terete in basal and median sectors, the distal sector obscurely trigonous and with 3 plicae, the perianth narrowing toward the contracted mouth; mouth cells thick-walled, often sinuate, partially or wholly laterally free, occasionally with a laterally free uniseriate row of 2 cells, the mouth thus indistinctly denticulate-subfimbriate; perianth 2- to locally 3-stratose in basal portion.

Seta with 8 rows of outer cells surrounding an inner core of 21–24 much smaller cells. Capsule rather short-ellipsoidal, 525 μm wide, 1070 μm long, the wall 41–46 μm thick, of 4 layers, the outer layer equivalent to 1.5–1.8× thickness of any one of the interior layers; outer layer of cells rather regularly short-rectangular, with two-phase development, the longitudinal walls with well-defined sheet-like thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, pigmented or non-pigmented, nodular

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lular detail. 6. Stem, cross section. 7, 8. Dorsal lobe and dorsal margin of disc. 9. Antheridial stalk. (Figs. 1, 2, 7, from holotype of var. *ampliata*; 3, from *Kirk 183*, New Zealand, Great Barrier Is.; 4, 5, 9, from *Zotov*, New Zealand, North Is., Southern North Is. EP, Tararua Ra., Field Hut; 6, 8, from *Hatcher 29*, New Zealand, North Is., Volcanic Plateau EP, Rotorua.)

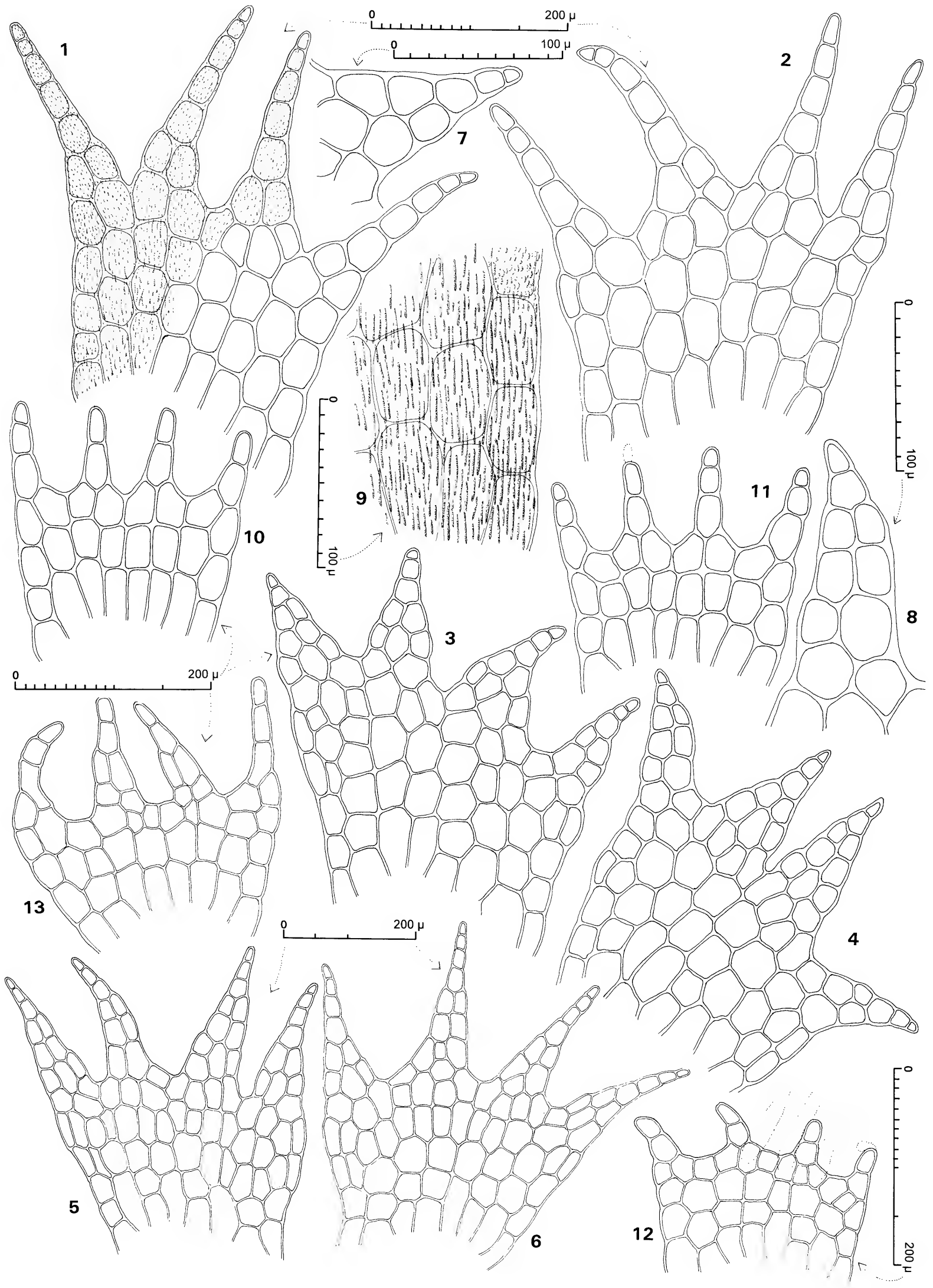

Fig. 60.
Telaranea patentissima (Hook.f. & Taylor) E.A.Hodgs. (figs. 1, 2, 9–11, var. *zebrina*; 3–8, 12, 13, var. *patentissima*). 1–6. Leaves, the leaf of fig. 1 with surface detail shown in part. 7, 8. Leaf lobes.

swellings), the transverse walls often with thickenings; innermost layer of cells ± tiered, irregularly narrowly to broadly rectangular, with semiannular bands common, rather wide, close, usually complete, rarely forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 12–13.9(15.4) μm in diam., the wall pale brown, with low but sharply defined, close papillae and short-vermiculate markings that at times coalesce. Elaters rigid, nontortuous, 8.6–10.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.4–3.8 μm wide.

Distribution and Ecology: New Zealand: Auckland Islands, Campbell Island, Stewart Island (0–200 m), South Island ([60]215–1900 m), North Island ([95]280–1350 m); Australia: Tasmania, New South Wales. In New Zealand known from Fiordland, Southland, Otago, Westland, Canterbury (near Main Divide), Western Nelson, Southern North Island (Tararua Ra.), Volcanic Plateau, Auckland and Northland EPs.

A rather common species throughout New Zealand and occurs in middle- to upper-elevation forests (typically above 400 m) to the penalpine–alpine zone. In the forest zone (often *Nothofagus*) it often occurs on very rotted logs, typically on the side or lower half of prostrate, bryophyte-covered logs, or in moist, sheltered niches such as cliff faces and soil of boulders of stream edges, etc. In the penalpine and alpine zones it occurs under snow tussock cover or over soil in protected niches of cliffs, etc. In Fiordland (Milford Sound) it was found at sea level with *Treubia lacunosa*, *Verdoornia succulenta* and *Geocalyx caledonicus*. It also, though rarely, occurs at lower elevations in pakihi (under *Gleichenia*).

Comments: *Telaranea patentissima* is a relatively common plant in New Zealand, but its variability may cause difficulties in determination. At times the species can resemble a smaller *T. tetrapila*. The leaf disc is ± regularly cuneate, with the disc cells arranged in regular rows and tiers (Fig. 59: 4). Another feature shared with *T. tetrapila* and its varieties is the occasional occurrence of secondary cell divisions at the tips of the lobes (Fig. 59: 3). However, the smaller plant size, the relatively small cells (40 μm in width or less), and the firm, rather evenly thickened cell walls, with small, but distinct trigones ally this species with sect. *Neolepidozia*.

For comments on nomenclature see Engel and Merrill (2004).

The species may be divided into three varieties as follows.

Key to the varieties of *T. patentissima*

1a. Leaf disc typically 4 cells high, ± regularly cuneate, the areolation regular, the cell divisions in distal sector mostly longitudinal, preserving a regular tiered arrangement; disc and lobe margins straight; leaves 4-lobed 2

2a. Cells of disc coarsely striolate-papillose; uniseriate portion of leaf lobes (4)5 cells long; underleaf disc 8 cells wide throughout, the lobes uniseriate, 2–3 cells long . . . . . var. *zebrina* (p. 300)

2b. Cells of disc smooth; uniseriate portion of leaf lobes 2–4(5) cells long; underleaf disc (8)10–14 cells wide in distal portion narrowing to 8 cells wide at base . . . . . var. *patentissima* (p. 300)

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9. Marginal cells of leaf base showing papillae. 10–13. Underleaves (all drawn to scale of fig. 10). (Figs. 1, 2, 9–11, from type of var. *zebrina*; 3, 4, 7, 8, 12, from type of *T. patentissima* [BM]; 5, 6, 13, from type of *T. gottscheana* [W].)

1b. Leaf disc typically 5–6(7) cells high, becoming irregularly and often asymmetrically cuneate, the areolation (especially in distal sector) ± irregular due to divisions in various planes; disc and lobe margins irregular, with bulging cells; leaves often 5–6-lobed . . . . . var. *ampliata* (p. 300)

Telaranea patentissima (Hook.f. & Taylor) E.A.Hodgs. var. ***patentissima***

[Fig. 59: 3–5, 9; Fig. 60: 3–8, 12, 13]

Lepidozia gottscheana Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 206. 1845. *Mastigophora gottscheana* (Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Neolepidozia gottscheana* (Lindenb.) Fulford & J.Taylor, Brittonia 11: 85. 1959. *Telaranea gottscheana* (Lindenb.) E.A.Hodgs., Rec. Domin. Mus. 4: 106. 1962. Type: New Zealand, Dusky Bay, "(Hb. Hk., L. et Lg. n. 28)," *sin. coll. – c. per.* + *sporo*. (G!, W!, Lindenberg Hepat. no. 4748).

Lepidozia gracillima Carrington & Pearson, Proc. Linn. Soc. New South Wales ser. 2. 2: 1045. *pl. XXVII*. 1888. Type: Australia, New South Wales, "New Sydney," Botany Bay, *Whitelegge – c.* ♂ (G!).

Lepidozia corticola Steph., Sp. Hepat. 3: 591. 1909. *Neolepidozia corticola* (Steph.) Fulford & J.Taylor, Brittonia 11: 85. 1959. *Telaranea corticola* (Steph.) E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. Type: New Zealand, South Is., Mt. Winterslow, (Canterbury), Mar. 1906, *Beckett 457* (G!); isotype: (CHR 585838 ex herb. Beckett!).

Leaves 4-lobed, the disc ± regularly cuneate, the disc and lobe margins straight; disc typically 4 cells high, with areolation regular, the cell divisions in distal sector mostly longitudinal, preserving a regular tiered arrangement.

Telaranea patentissima var. ***ampliata*** J.J.Engel & Merrill

[Fig. 59: 1, 2, 6–8]

Telaranea patentissima var. *ampliata* J.J.Engel & Merrill, Fieldiana, Bot. 44: 48. *f. 16: 1, 2, 6–8.* 2004. Holotype: New Zealand, Otago Prov., Mt. Maungatua, W of Mosgiel, 500 m, *Engel 17777 – c. sporo.* (F); isotype: (CHR).

Leaves often 5–6-lobed, the disc becoming irregularly and often asymmetrically cuneate, the disc and lobe margins irregular, with bulging cells; disc typically 5–6(7) cells high, with areolation (especially in distal sector) ± irregular due to divisions in various planes.

This distinctive expression of the species has broad, somewhat irregularly cuneate leaves, with the cells of the lobe and disc margins often bulging (Fig. 59: 7, 8). The leaf disc is rather high (to 6 or 7 cells, Fig. 59: 2), the cells are somewhat irregularly arranged, and the lobes are narrowly acute (often 3–4 cells wide for several tiers above the extreme base).

Telaranea patentissima var. ***zebrina*** J.J.Engel & Merrill

[Fig. 60: 1, 2, 9–11]

Telaranea patentissima var. *zebrina* J.J.Engel & Merrill, Fieldiana, Bot. 44: 50. *f. 17: 1, 2, 9–11.* 2004. Holotype: New Zealand, North Is., Puketi Forest, 6 Dec. 1993, *Braggins 93/172* (AKU); isotype: (F).

Leaves distinctly papillose, the dorsal half of disc coarsely striolate-papillose, the lobes with a uniseriate row (4)5 cells long (more than half the length of lobe); underleaf disc 8 cells wide throughout, the lobes uniseriate, 2–3 cells long.

This variety is similar to var. *patentissima* in almost all respects, but has a more pronounced development of surface papillae on the leaves. Papillae are not confined to the tips of the lobes, but occur also on the disc (Fig. 60: 1), which is conspicuously striolate (Fig. 60: 9).

Telaranea tetrapila (Hook.f. & Taylor) J.J.Engel & Merrill

[Fig. 50: 6, oil-bodies, p. 268; Figs. 61, 62: 1–3, 9–12; Fig. 67: 5, oil-bodies, p. 322]

Lepidozia tetrapila Hook.f. & Taylor *in* Taylor, London J. Bot. 5: 370. 1846. *Mastigophora tetrapila* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Telaranea tetrapila* (Hook.f. & Taylor) J.J.Engel & Merrill, Phytologia 79: 253. June 1996 (1995). Lectotype: New Zealand, *Hooker* "n. 119. 1844" (FH!); isolectotype: (W!, Lindenberg Hep. no. 4739).

Plants soft, flexuous yet firm, loosely prostrate to suberect, in dense, compact mats, pale green to yellowish green to olive-green (to pale amber in var. *cancellata*), nitid when dry, often somewhat water-repellent; plants variable in stature, small to medium, to 1.5 cm wide, including branches. Branching regular and rather densely 1-pinnate, sometimes 2-pinnate, at times plumose in robust plants, the branches of the *Frullania* type; branch half-leaf 2(4)-lobed, narrowly rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided and ciliiform or, less often, bifid, sporadically trifid, inserted on ventral side of branch near or (often) at juncture of branch and main axis. Ventral-intercalary branches occasional, leafy, often becoming leading shoots. Stems with cortical cells distinctly differentiated, thin-walled, in 11–18 rows; cortical cells in section much larger than the numerous 35–65 medullary cells. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rigid, obliquely spreading, distant (small phases) to loosely to closely imbricate, plane to moderately convex, the insertion weakly to distinctly incubous; leaves 630–980 μm wide × 630–840 μm long, subsymmetric, 4–6(8)-lobed to 0.4–0.55, typically shorter than the disc (longer than the disc in var. *cancellata*). Lobes typically subcaudate, the base subtriangular, 2–4 cells wide at extreme base, terminating in a uniseriate row of (4)5–6(8) cells (typically more than half the length of lobe); cells of the uniseriate portion short, often ± barrel-shaped (longer cells of the uniseriate portion to 2.5:1 in var. *cancellata*), rather thin-walled, the septa thickened in the corners but the septa not swollen and projecting, the distal lobe cells often short-quadrate and more numerous resulting from secondary cell divisions; surface of at least the distal half of lobes finely to ± distinctly striate-papillose. Disc symmetrically to somewhat asymmetrically broadly subrectangular to cuneate, 4–6(7) cells high (from median sinus base to leaf base), (9)14–21 cells wide in distal portion narrowing to 8–12 cells wide in basal portion (disc typically 8 cells wide throughout in var. *roseana*); cells of disc margins often bulging. Cells of disc thin-walled but firm, trigones lacking or minute, large, convex, pillow-like (obvious even under low magnification), the largest cells (in median sector of disc) large, often ± isodiametric, (45)50–70 μm wide × 55–90 μm long; basal 1–2 rows of disc cells considerably larger (wider), irregularly arranged or in ± regular tiers; cells of disc margins (especially the dorsal) sometimes forming an indistinct border of elongate, narrower cells; surface smooth. Oil-bodies greyish (var. *tetrapila*) or hyaline (var. *cancellata*), coarsely papillose, the spherules protruding beyond membrane, the median disc cells with 5–11 oil-bodies per cell (8–9 in lobe cells), narrowly to broadly

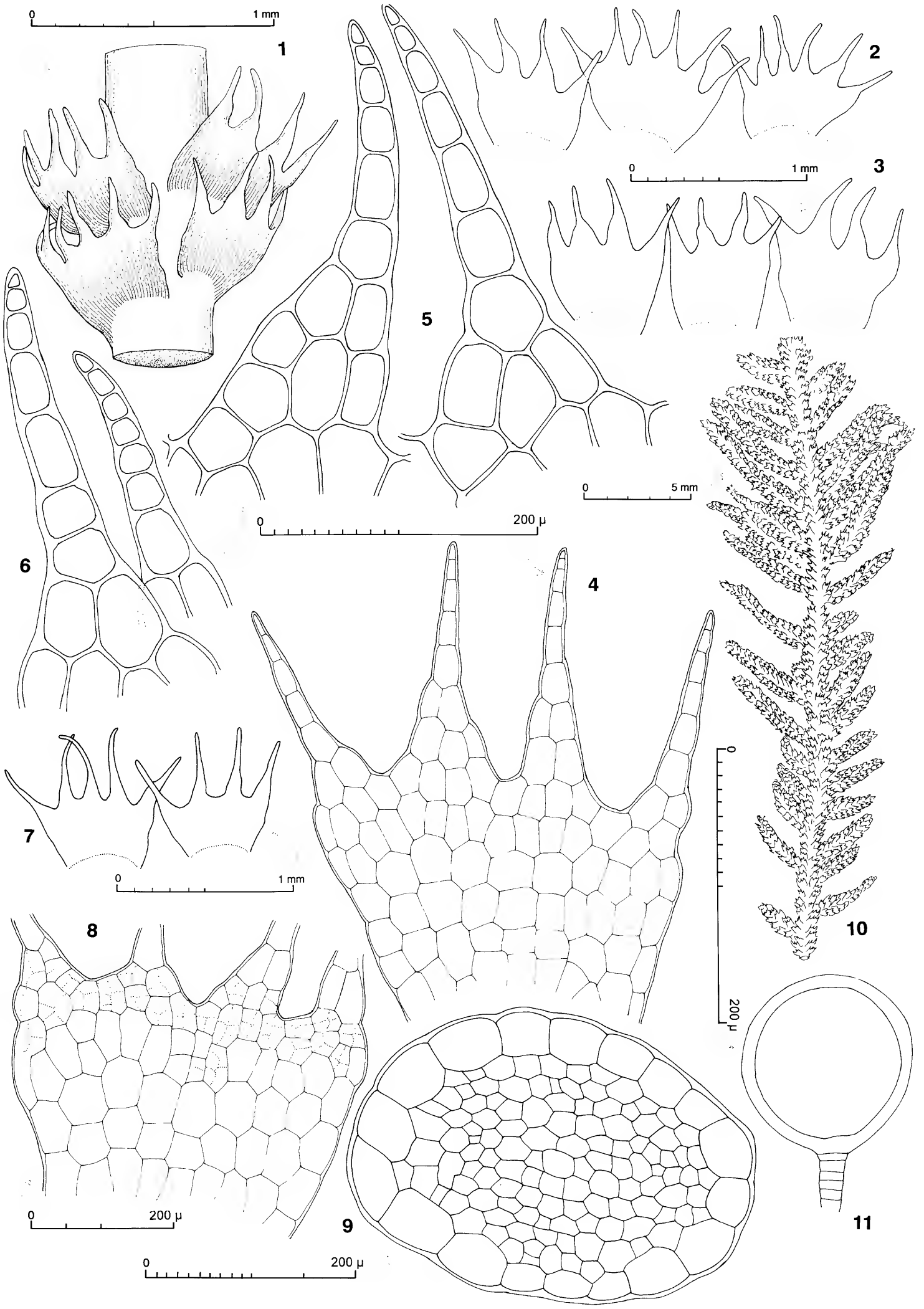

Fig. 61.
Telaranea tetrapila (Hook.f. & Taylor) J.J.Engel & Merrill var. *tetrapila*. 1. Sector of leading shoot, dorsal view. 2, 3. Leaves. 4. Leaf, cellular detail. 5, 6. Median lobes of leaf; note secondary septa. 7. Underleaves. 8. Underleaf disc, cellular detail, stippled cell walls indicate rhizoid initial cells. 9.

elliptic to subcrescentic and 5.5–5.8 × 8.3–11.6 μm, less often ca. 5.3 × 14.7 μm, the subspherical ones 5.9–6.6 μm in diam. Underleaves normally smaller than leaves (subequal to leaves in var. *cancellata*), strongly spreading, contiguous to loosely imbricate, plane, 4–6-lobed to 0.4–0.6, the lobes ciliiform, the uniseriate portion formed of 3–5(8) somewhat elongated cells; disc symmetrically cuneate, (3)4–5 cells high (median sinus), the cells in ± regular tiers or irregularly arranged, the disc (10)12–19 cells wide in distal portion narrowing to 8–10 cells wide at base. Rhizoid initial cells small, subquadrate, at bases of lobes or forming a continuous bistratose band across the apex of the disc. Asexual reproduction lacking. Fungal partner an ascomycete.

Plants dioecious. Androecia on short, abbreviated, ventral-intercalary branches from leading shoots, as well as from flagelliform or stoloniform branches; bracts closely imbricate, dorsally assurgent, deeply concave, 2–3-lobed, each lobe terminating in a single cell or a uniseriate row of 2 not to hardly elongated cells; lamina cells irregular in shape and arrangement, the dorsal margin of lamina feebly dilated and slightly incurved, irregularly crenulate, at times with a few sessile slime papillae; bracts monandrous; antheridia large for bract size, the stalk short, ca. 7 cells high, uniseriate; bracteolar antheridia absent. Gynoecia with bracts and bracteoles in 2–3 series, inserted on the vestigial perigynium, becoming progressively larger and less deeply lobate toward the perianth, those of innermost deeply concave, the apical portion canaliculate; bracts of innermost series ± suborbicular, irregularly 4-lobulate, the lobules terminating in a uniseriate row of 1–2 cells; bract margins crenate to dentate, the armature frequently sharply inflexed, often terminating in a slime papilla, the bracts with an obscure border formed of 1 to several rows of cells longer, narrower and more irregular than those within; bracteoles nearly identical in form to bracts although a little smaller, free from bracts. Perianth not extending above vegetative axes, 0.5–0.55 emergent, ovoid-cylindrical, terete in basal half, the distal half obscurely trigonous and with 6–9 plicae, the sulci shallow to deep; perianth narrowed toward a decidedly contracted mouth, the mouth with 6 narrowly triangular lobes, each lobe fringed with slightly thick-walled, contorted, crowded, sparingly papillose cilia, the terminal cell of each cilium coarsely papillose.

Seta with 8–9 rows of outer cells surrounding an inner core of 20–34 much smaller cells. Capsule short-cylindrical, 560–805 μm wide, 1204–1470 μm long, the wall 41–50 μm thick, of 4 layers (locally 3), the outer layer subequal to the combined thickness of the inner layers, or slightly less thick; outer layer of cells in tiers, ± regularly short-rectangular, with two-phase development rather indistinct, the longitudinal secondary walls with sheet-like thickenings and nodule- to spine-like thickenings (4–6 per cell) alternating with primary walls also with similar thickenings, the transverse walls almost devoid of thickenings, or with local, non-pigmented, nodular swellings; innermost layer of cells ± tiered, rather regularly narrowly rectangular, with semiannular bands common, rather narrow, complete, only rarely forked to delimit local fenestrae.

Spores 12–13.4 μm in diam., the wall rather thick in optical section, dark yellow-brown, areolate (with a low, close network of well-defined, rather thick, furcate ridges that anasto-

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Stem, cross section. 10. Plant, dorsal view. 11. Antheridium (as seen in optical section). (Figs. 1, 3, 6, 7, 10, from *J.J.Engel 18029*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, summit area of Haast Pass; 2, 5, 8, from *Reif C151A*; 4, from *Reif C93E*; 9, from *Reif C80F*, all Reif coll. from New Zealand, South Is., Westland EP, Camp Creek; 11, from *Engel 19298*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., Croesus Track.)

mose to form areolae). Elaters rigid, ± straight, 9.1–12.5 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.8–5.3 μm wide.

Comments: *Telaranea tetrapila* is the oldest name for the species that has generally been called *Telaranea* (or *Lepidozia*) *gottscheana* in the New Zealand literature (e.g., Hodgson, 1956; Allison and Child, 1975). The type of the name *L. gottscheana*, however, is *T. patentissima*. At its best, *T. tetrapila* is one of the most handsome of our *Telaranea* species, and is common throughout New Zealand. The plants are highly variable in size, color, and general aspect, as well as leaf form and number of lobes. The most useful features for distinguishing the species are the large, pillow-like, almost geometrically hexagonal disc cells (Fig. 61: 4; Fig. 62: 3), which are conspicuous and easily observed, even under the dissecting microscope, the bulging cells of the lobe bases and the short, secondarily divided cells at the lobe tips (Fig. 61: 5, 6; Fig. 62: 9). One marked expression of *T. tetrapila* (var. *roseana*) bears a strong resemblance to *T. tuberifera*, due to its widely spreading, parallel-sided leaves (Fig. 62: 1). Another (var. *cancellata*) somewhat resembles *T. gibbsiana* in the finely elongated leaf lobes, and large, ciliiform-lobed underleaves.

Telaranea tetrapila has often been confused with *T. praenitens*, which differs by its more deeply lobed, palmate leaves and the characteristic minute denticulations formed by the swollen projecting end-walls on the lobes and disc margins.

Key to the varieties of *T. tetrapila*

1a. Leaves rather flat and widely spreading, the disc parallel-sided and somewhat higher than wide (resembling *T. tuberifera*), 8 cells wide in both distal and basal portions; lobes often straight and aligned with the disc margins . . . . . var. *roseana* (p. 304)

1b. Leaves weakly to distinctly convex and obliquely spreading, the disc weakly to distinctly cuneate, (9)14–21 cells broad distally, the margins often curved; lobes divergent 2

2a. Lobes typically shorter than the disc, the cells of the uniseriate row short, often ± barrel-shaped; underleaves smaller than leaves; oil-bodies greyish, 5–8 per cell. Common throughout New Zealand . . . . . var. *tetrapila* (p. 307)

2b. Lobes longer than the disc, the cells of the uniseriate row ± elongate (to 2.5:1), not barrel-shaped; underleaves subequal to leaves in size; oil-bodies hyaline, 8–11 per cell. Scattered sites in the North Is. . . . . var. *cancellata* (p. 305)

Telaranea tetrapila var. ***roseana*** (Steph.) J.J.Engel & Merrill

[Fig. 62: 1–3]

Lepidozia roseana Steph., Sp. Hepat. 3: 590. 1909. *Neolepidozia roseana* (Steph.) Fulford & J.Taylor, Brittonia 11: 85. 1959. *Telaranea roseana* (Steph.) E.A.Hodgs., Rec. Domin. Mus. 4: 106. 1962. *Telaranea tetrapila* var. *roseana* (Steph.) J.J.Engel & Merrill, Phytologia 79: 253. June 1996 (1995). Type: New Zealand, without specific loc., 1898, *Petrie*, "com. Rose" (G!).

Plants resembling *Telaranea tuberifera*; leaves rather flat and widely spreading; leaf lobes typically shorter than the disc, subcaudate, ± parallel with the disc margins; leaf disc parallel-sided and somewhat higher than wide, typically 8 cells wide in both distal and basal portions, the cells conspicuously large, hexagonal (as in var. *tetrapila*).

Distribution and Ecology: Endemic to New Zealand: South Island (125–455 m), North Island (150–800 m). Known from Fiordland, Southland, Otago, Westland, Western Nelson, Volcanic Plateau (Tongariro Natl. Park), Auckland (Whareorino Forest, Coromandel Forest Park) and Northland (Waipoua) EPs.

The var. *roseana* is known primarily from South Island in lower- to middle-elevation forests, especially on damp, clayey banks.

Comments: Plants assigned to this variety often bear a striking resemblance to *Telaranea tuberifera*, but differ by not having the glaucous surface or the strongly horizontal leaf orientation of that species; it also differs by the non-fragmenting lobe apices and the absence of tubers at the tips of flagelliform stolons. The leaves are obliquely oriented, as in var. *tetrapila*, but are typically rather flat, and diverging at a wider angle with the stem. As indicated in the species description, *T. tetrapila* is very variable, and even well-developed plants will have some leaves that are only 8 cells wide throughout the disc, particularly on the branches. The var. *roseana*, when well developed, has a very characteristic appearance, due to the conspicuously parallel-sided disc (somewhat higher than wide), which is typically 8 cells wide in both distal and basal portions (Fig. 62: 3), and the lobes are often straight and aligned with the disc margins.

The var. *roseana* differs from *Telaranea paludicola* by the more slender lobes, which are 2 (and only sporadically 3–4) cells wide at the base, and the very prominent, hexagonal disc cells are arranged in precise geometrical fashion.

Telaranea tetrapila var. ***cancellata*** (Colenso) J.J.Engel & Merrill

[Fig. 50: 6, oil-bodies, p. 268; Fig. 62: 9–12]

Lepidozia cancellata Colenso, Trans. & Proc. New Zealand Inst. 18: 244. 1886. *Telaranea tetrapila* var. *cancellata* (Colenso) J.J.Engel & Merrill, Phytologia 79: 253. June 1996 (1995). Type: New Zealand, Waipawa Co., near Norsewood, edge of Bartramia Creek, 1885, *Colenso a. 1418* (BM!, WELT!).

Psiloclada digitata Colenso, Trans. & Proc. New Zealand Inst. 18: 243. 1886. Type: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1378* (BM!, WELT – *absens*).

Plants resembling *Telaranea gibbsiana*, often pale amber in color; plants medium, to 1.1 cm wide, including branches; branching somewhat irregularly to regularly 1-pinnate; leaf lobes longer than the disc, subcaudate, rather abruptly tapering to a uniseriate row of cells, ± straight, the cells of the uniseriate row ± elongate (to 2.5:1), not barrel-shaped; leaf disc at most moderately asymmetric, the disc cells mostly isodiametric; oil-bodies greyish, 5–8 per cell; underleaves subequal to the leaves in size, with long, ciliiform lobes, the terminal cells often secondarily divided.

Distribution and Ecology: Endemic to New Zealand: North Island (245–1160 m). Known from Southern North Island (Tararua Ra.), Gisborne (Urewera Natl. Park) and Auckland (Herangi Ra., Mt. Te Aroha, Great Barrier Island) EPs.

Known only from several scattered sites, "on trees and logs, forming large and thick patches" (Colenso, *loc. cit.*, p. 245). On Mt. Te Aroha, plants occurred at 880–890 m loosely on the floor as well as over soil deep in a protected niche under the lip of the forest overhang, both populations in a stunted *Nothofagus menziesii* forest associated with *Dracophyllum* and *Quintinia serrata*. In the Herangi Ra. (S of Kawhia Harbor) the species occurred at ca. 720–750 m on an exposed plateau with a mosaic of penalpine bog vegetation, stunted *Quintinia ser-*

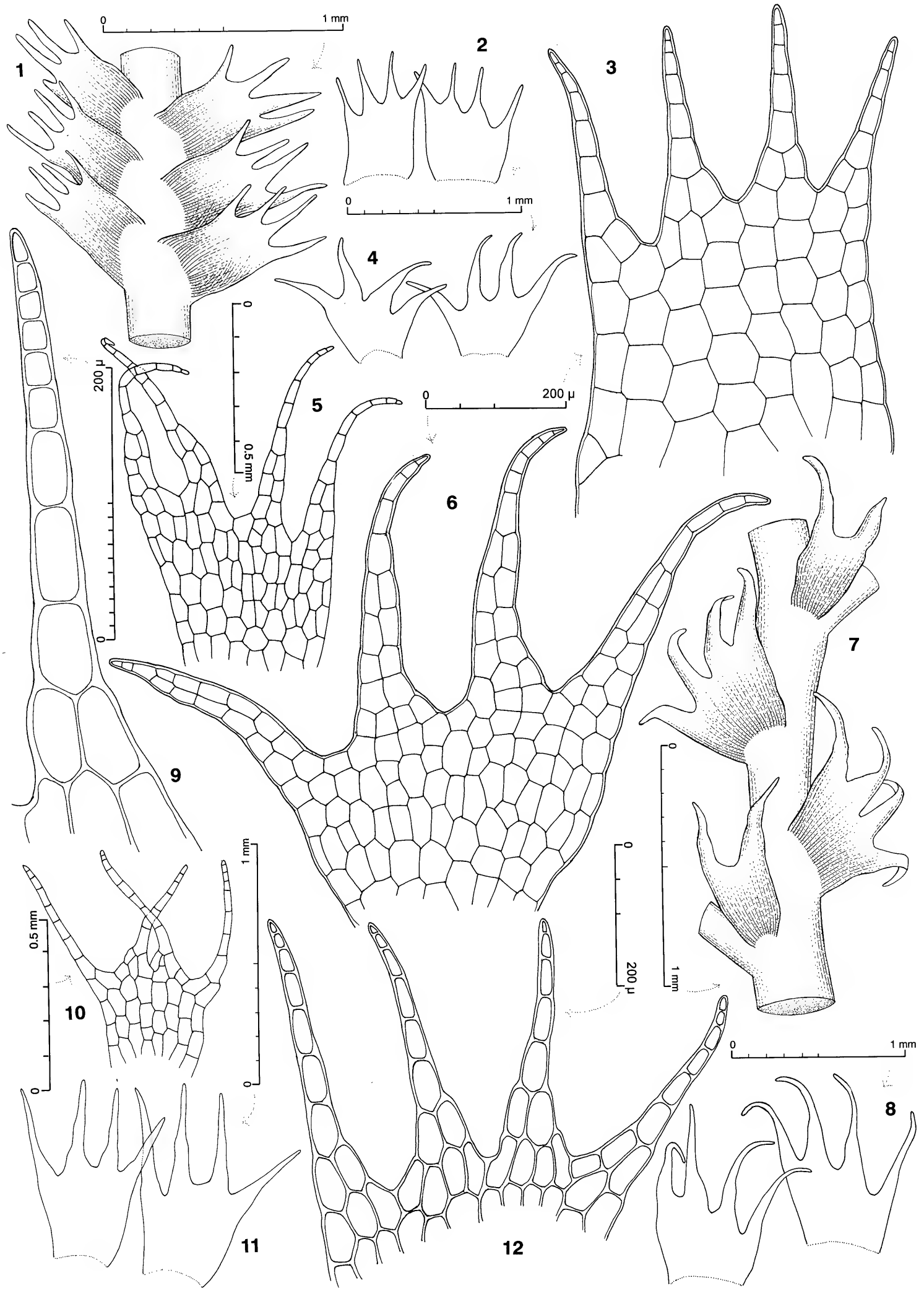

Fig. 62.
Telaranea tetrapila (Hook.f. & Taylor) J.J.Engel & Merrill var. *roseana* (Steph.) J.J.Engel & Merrill (1–3); var. *cancellata* (Colenso) J.J.Engel & Merrill (9–12); *Telaranea paludicola* (E.A.Hodgs.) E.A.Hodgs. (4–8). 1. Sector of main shoot, dorsal view. 2. Leaves. 3. Leaf, cellular detail. 4. Leaves. 5, 6. Leaves, cellular detail. 7. Sector of main shoot with branch bases and associated half-leaves, dorsal view. 8. Leaves of extreme. 9. Leaf lobe showing secondary cell divisions

rata and *Dracophyllum* heath (to 1 m tall), rocky outcrops and small water channels. At this site plants were found in moist niches, e.g., on the floor or beneath blades of *Poa* sp.

Comments: Colenso (1886a, p. 245) aptly described this as "a truly elegant plant." It is chiefly distinguished by the rather regularly 1-pinnate shoots; the often pale amber pigmentation; the slender leaf lobes, which are subcaudate as in the var. *tetrapila*, but with a uniseriate row composed of elongated (to 2.5:1) cells; and the rather large underleaves, with long, ciliiform lobes, rather like those of *Telaranea gibbsiana*. It differs from *T. paludicola* in the ± isodiametric cells of the disc and lobe bases, and the abruptly tapering lobes, with a long, uniseriate row, which are ± straight, vs. lobes biseriate, often falcate and hooked at the tips in *T. paludicola*.

Telaranea tetrapila (Hook.f. & Taylor) J.J.Engel & Merrill var. ***tetrapila***

[Fig. 61; Fig. 67: 5, oil-bodies, p. 322]

Plants with shoots to 1.5 cm wide (including branches); branching regularly and rather densely pinnate (often plumose in well-developed plants); leaf lobes typically shorter than the disc, subcaudate, ± straight, the cells rather short, barrel-shaped; leaf disc at most moderately asymmetric, often distinctly cuneate, (9)14–21 cells broad distally, composed mostly of large, hexagonal cells, except for distal tier at base of lobes; oil-bodies hyaline, 8–11 per cell.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (10–530 m), South Island (0–1280 m), North Island (60–1370 m), Chatham Islands. Known from all ecological provinces in North and South islands.

The typical variety is common throughout our area in low- to middle-elevation forests (typically below 700 m), where it can be particularly luxuriant. It can occur in the upper limits of *Nothofagus menziesii* forests, or in penalpine scrub, but at these upper elevations, the plants often represent a small or weak phase of the species (it nevertheless may produce sporophytes and androecia and may be well developed in such niches). It grows on an array of substrates, but typically can be found on the forest floor, on soil of mossy banks, on rotted logs or, at times, on upright tree trunks. It is able to tolerate some degree of exposure, and can occur, for example, in open boggy areas with *Juncus squarrosus*, *Coprosma*, *Leptospermum scoparium* and *Ozothamnus leptophyllus* (Mt. Cargill, Otago), or in pakihi, with *Gleichenia*, *Lycopodium*, *Juncus*, *Drosera* spp., *Schizaea* and *Leptospermum* (Tiropahi River, Westland).

Telaranea paludicola (E.A.Hodgs.) E.A.Hodgs.

[Fig. 62: 4–8]

Lepidozia meridiana var. *paludicola* E.A.Hodgs., Trans. Roy. Soc. New Zealand 83: 611. *pl. 2, f. 21*. 1956. *Telaranea paludicola* (E.A.Hodgs.) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 69. 1965; J.J.Engel & Merrill, Phytologia 79: 252. 1996 (1995). Holotype: New Zealand,

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in distal portion. 10. Underleaf. 11. Leaves (note, figure drawn at 50% larger than other leaf outlines). 12. Distal sector of leaf. (Figs. 1–3, from *Fife 4964*, New Zealand, South Is., Western Nelson EP, Fox R.; 4, 6, 7, from type of *L. paludicola*; 5, 8, from *Child 5446*, New Zealand, South Is., Western Nelson EP, Big Totara R.; 9–12, from *Zotov 7083*, New Zealand, North Is., Southern North Is. EP, Ohauiti R.)

North Is., Tararuas, Oriwa Lake Hollow, bog, 3300 ft., 15 April 1933, *Zotov* (CHR!; "No. 6619 in Bot. Divn. Herb."); isotype: (MPN, Hodgson herb. no. 1193, *non vidi*).

Plants with a rather spinose appearance, resembling *Telaranea praenitens*, soft, flexuous yet firm, loosely prostrate, often in dense, compact mats, pale green to olive-green or at times brownish yellow to rust-brown, nitid when dry; shoots medium, to 0.9 cm wide, including branches. Branching somewhat irregularly to regularly 1-pinnate, the branches of the *Frullania* type, often flagelliform; branch half-leaf 2(3–4)-lobed, narrowly rectangular to linear, the lobes parallel to slightly diverging; first branch underleaf undivided and ciliiform or less often 2–3-lobed, inserted on ventral or ventral-lateral side of branch near base. Ventral-intercalary branches occasional, often becoming leading shoots and leafy throughout. Stems with cortical cells markedly differentiated, the radial walls thin, the outer wall slightly thickened, in 12–14 rows; cortical cells in section larger than the numerous (ca. 65) medullary cells. Leaves on main shoot rigid, distant to loosely imbricate, widely spreading, moderately concave, the lobes incurved, the insertion moderately incubous; leaves 770–980(1260) μm wide (from lobe tip to lobe tip) × 700–1050 μm long, usually distinctly asymmetric, or less often subsymmetric, ± equally 4(5–6)-lobed to ca. 0.4–0.6, the lobes typically somewhat longer than the disc, often distinctly falcate and hooked at the tip. Lobes slender, long-attenuate, divergent, the dorsal lobes often ± paired, the lobes 3–4 cells wide for 1–2 tiers at extreme base, biseriate for 2–4(5) tiers, terminating in a long uniseriate row of (4)5–7(8) cells (at times more than half the length of lobe); lobe cells ± firm, thin to moderately thickened, the septa thickened in the corners but not swollen and projecting from the lobe margins (the lobes at times somewhat constricted at the septum), the lobe cells all elongated (to 2.5:1); surface smooth or finely striate-papillose at lobe tips. Disc often distinctly asymmetric, typically longer than broad and narrowing to the base, 5–7 cells high (from median sinus base to leaf base), 15–16 cells wide in distal portion narrowing to 8–11 cells wide in basal portion; disc margins entire, or the marginal cells somewhat bulging. Cells of disc moderately thin-walled, trigones small or lacking, median disc cells longitudinally elongate, (38)45–52 μm wide × 65–110 μm long, in ± regular, somewhat obliquely arranged tiers; surface smooth. Underleaves much smaller than leaves, strongly spreading to subsquarrose, distant, plane, 4(5)-lobed to ca. 0.6, the lobes ciliiform, straight to subfalcate and hooked at tip, 2 cells wide at the base, often with an additional biseriate tier at base of lobe, the uniseriate portion formed of (3)5–8 short to elongated cells with septa thickened at the corners; disc symmetrically cuneate, 4–5(6) cells high (median sinus), the cells in ± regular tiers; disc 9–12 cells wide in distal portion narrowing to 8 cells wide at base. Rhizoid initial cells small, subquadrate, at bases of lobes or forming a continuous bistratose, dense band across the apex of the disc.

Gametangia and sporophytes not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5 m), South Island (60–1480 m), North Island (305–1320 m). Known from Fiordland, Southland, Otago, Westland, Canterbury (Arthur's Pass), Western Nelson, Sounds–Nelson, Southern North Island, Taranaki, Volcanic Plateau and Northland EPs.

Sporadic in distribution in middle and upper elevations (usually not below 500 m) of both South and North islands. As the specific epithet suggests, the plants typically occur in boggy sites, at times creeping among *Sphagnum cristatum* (for example, on the sides of old *Sphagnum* mounds, or mixed with *Chiloscyphus spiniferus* deep in shaded pockets among bryophyte masses). At Omoeroa Saddle it occurred in a bog with dwarf shrub heath vegetation including *Juncus*, *Carex* and stunted *Libocedrus bidwillii* surrounded by mature *Dacrydium cupressinum* forest. In penalpine areas it occurs in sheltered, protected pockets, particularly in moist

sites, such as rills in scrub consisting of *Chionochloa*, *Dracophyllum* and *Hebe* or of *Dracophyllum* and *Olearia colensoi*; also found under cover of tussock blades in mosaic areas of stunted *O. colensoi* and *Chionochloa*. Also at the lips of tarns in low alpine vegetation (Mt. Robert Skifield, Nelson Lakes Natl. Park).

The species also is present on Stewart Island, but as is the case with a number of vascular and nonvascular plants, it occurs at considerably lower elevations on this island as compared to counterparts on the South and North islands (see Wardle, 1991). *Telaranea paludicola* was found at 5 m (track to Mason Bay) in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath (to 1–2 m tall) and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. At this site the species occurs in ± protected, moist niches, e.g., on the floor (particularly in pockets), on vertical, shaded small banks under *L. scoparium* or at the margin of bryophyte-covered mounds beneath *Leptospermum*. At Waiotapu Valley (Volcanic Plateau), it was found on a shaded damp bank with *Trichocolea rigida* and *Distichophyllum pulchellum*.

Comments: *Telaranea paludicola* is a striking plant when well developed. Although described as a variety of *T. meridiana* (Hodgson, 1956), *T. paludicola* has little to do with that species. It is more likely to be confused with *T. tetrapila*, but is distinguished primarily by the pronounced leaf asymmetry (Fig. 62: 5, 6, 8), the longitudinally elongated disc cells (Fig. 62: 5, 6), and the slender, caudate leaf lobes, which are often falcate and hooked at the tips (Fig. 62: 6–8).

Sect. ***Ceraceae*** J.J.Engel & Merrill

Telaranea sect. *Ceraceae* J.J.Engel & Merrill, Fieldiana, Bot. 44: 61. 2004. Type: *Lepidozia centipes* Taylor.

Telaranea sect. *Glaucolepidozia* R.M.Schust., Beih. Nova Hedwigia 118: 212. 2000, *nom. nud.*

Telaranea elegans (Colenso) J.J.Engel & Merrill

[Fig. 63: 1–6]

Lepidozia elegans Colenso, Trans. & Proc. New Zealand Inst. 21: 65. 1889 (1888). *Telaranea elegans* (Colenso) J.J.Engel & Merrill, Phytologia 79: 251. June 1996 (1995). Type: New Zealand, Great Barrier Is., Firth of Thames, 1888, *Winkelmann* (Colenso a.1355) (BM!, WELT!).

Lepidozia tripilosa Steph. *in* Steph. & Watts, J. Proc. Roy. Soc. N. S. W. 48: 116. 1914. Type: Australia, New South Wales, Centennial Glen, Blackheath, 10 Jan. 1911, *Watts 1043* (G!).

Plants delicate, flexuous, prostrate in loosely creeping, thin mats, faintly glaucous and water-repellent (particularly shoot tips), yellowish green to olive-green and ± nitid, becoming brownish with age; shoots medium, to 6 mm wide, including branches. Branching loosely but ± regularly and often sparingly pinnate, the branches of the *Frullania* type; branch half-leaf bifid, linear; first branch underleaf undivided, subulate, inserted on ventral-lateral side of branch near juncture of branch and main axis. Ventral-intercalary branches occasional, both stoloniform and leafy and becoming leading shoots. Stems with cortical cells thin-walled but firm, in 12 rows, in section much larger than the numerous (26–29) medullary cells. Rhizoids from distal cells of underleaf disc. Leaves on main shoot spreading at right angles to stem, approximate to contiguous but scarcely overlapping, plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion almost lon-

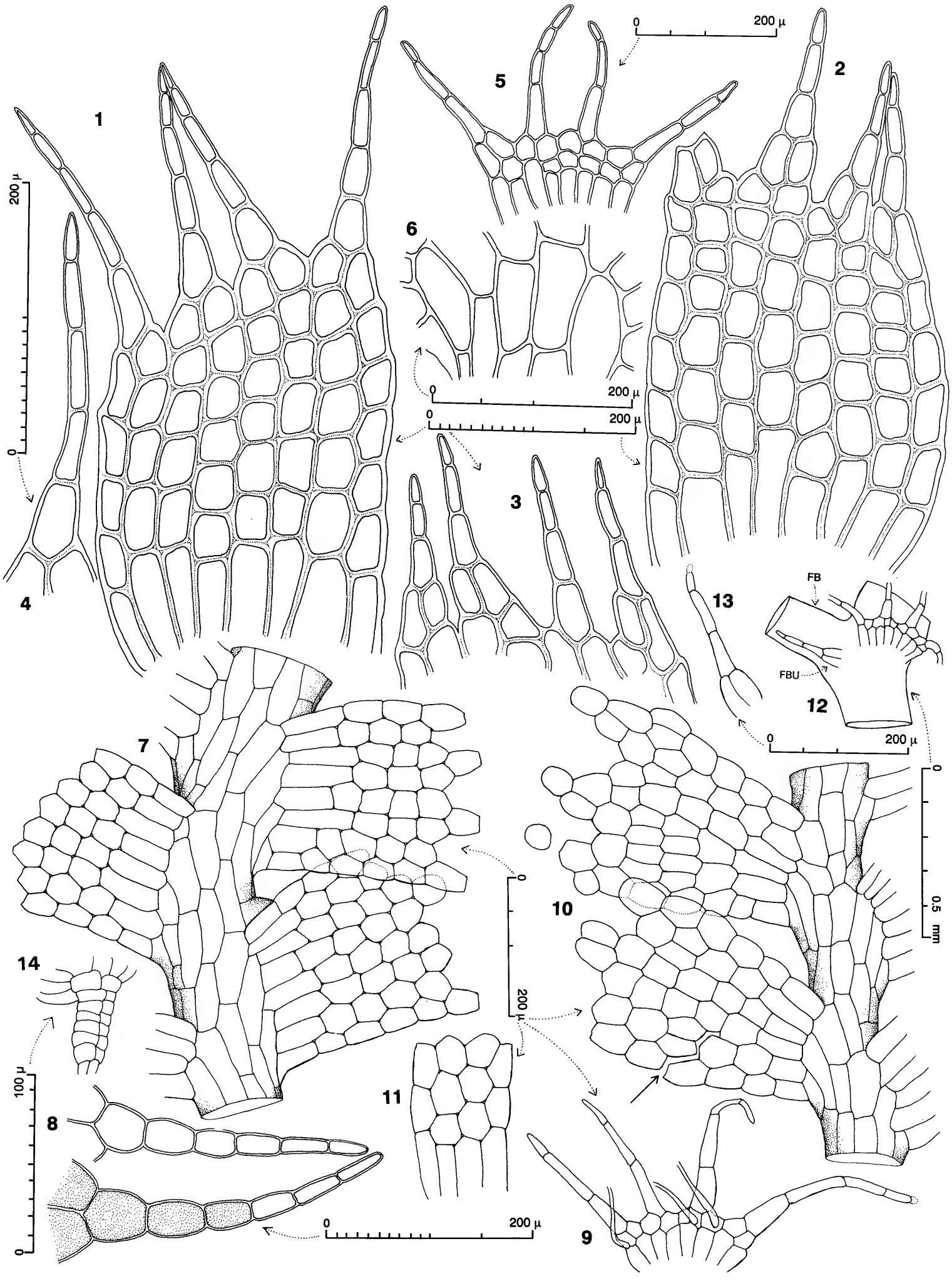

Fig. 63.
Telaranea elegans (Colenso) J.J.Engel & Merrill (1–6) and *T. perfragilis* J.J.Engel & Merrill (7–14). 1, 2. Leaves. 3. Distal portion of leaf. 4. Leaf lobe. 5. Underleaf. 6. Stem, surface view. 7. Sector of main shoot, dorsal view. 8. Leaf lobes (surface detail shown in part). 9. Underleaf. 10. Sector of branch showing (top leaf) fragmenting of leaf tip forming a gemma-like body (at arrow) and (lower leaf) a disc in process of partially breaking away (fracture at arrow). 11. Half-leaf. 12. Branch base (FB = *Frullania*-type branch; FBU = first branch underleaf), the underleaf of main shoot shown

gitudinal, the lobe tips often broken; leaves 200–285 μm wide × 385–575 μm long, longer than broad, (3)4-lobed to 0.4, the lobes strictly parallel with disc margins, shorter than the disc. Lobes setaceous, 2–3(4) cells wide at extreme base, uniseriate or biseriate in basal tier, the uniseriate portion 3–4 cells long, the lobe cells successively narrower in width (the cells scarcely tapered); cells of uniseriate portion elongate-rectangular, the walls straight-sided and not bulging. Disc ± symmetrically rectangular, parallel-sided, 5–6 cells high (from median sinus base to leaf base), 8 cells wide throughout; margins entire or finely serrulate by projecting distal ends of the marginal cells (especially the dorsal margin); ventral margin ± straight, the dorsal weakly arched. Cells of disc firm, in regular longitudinal rows, uniformly and often distinctly thick-walled, trigones none; median disc cells isodiametric to short-rectangular, 23–36 μm wide, 33–49 μm long; basal row of disc cells considerably longer and forming an obvious tier; surface with a hazy to faintly granular appearance, rarely glaucous. Underleaves much smaller than leaves, widely spreading, 4-lobed to 0.75–0.85, the lobes divergent, ciliiform, consisting of a uniseriate row of 2–3 elongated, thin- to slightly thick-walled cells, inserted on 2 disc cells, terminating in a slime papilla; disc abbreviated, 2(3) cells high, 8 cells wide. Asexual reproduction probably by broken tips of leaf lobes.

Gametangia and sporophytes not seen.

Distribution and Ecology: New Zealand: North Island ([60]290–940 m); Australia: New South Wales, Queensland.

In New Zealand known from a few stations in the northern sector of North Island (Waipoua Forest, Great Barrier Island, Coromandel Forest Park and the Kaimai Ra.). The New Zealand populations occur in *Nothofagus menziesii – Griselinia littoralis* forest or *Leptospermum scoparium – Weinmannia silvicola – Dacrydium cupressinum* short forest or (Waipoua area) *Agathis australis* forests with *W. silvicola*. At Aongatete River (Kaimai Ra.) the species occurred in a mixed *D. cupressinum* and *Beilschmiedia tawa* forest with a *Cyathea* understory. Plants occur in shaded, moist, protected niches, often with only marginal light, as, for example, within pockets on ± vertical stream banks. Plants for the most part are very loosely creeping, and form thin, ± pure, felt-like sheets that hardly touch the substrate. At Waikohatu Stream in Waipoua Forest the species occurs not only over soil under overhanging vertical banks well above the stream, but also, at this hyperhumid site, grows epiphytic on fronds of *Trichomanes elongatum*. The Waipoua plant collected by Allison formed a pure colony on very shady bare ground above a creek in the forest; the niche was "too shady for other plants" (label data).

Comments: This is an interesting species, both in its morphology and its disjunct geographical distribution. In overall aspect, leaf shape, and slender, bristle-like leaf lobes it resembles a small *Telaranea tuberifera* (p. 312), but the lobes in *T. elegans* are typically shorter, only 3–4 cells in length (Fig. 63: 2, 3) vs. (4)5–6(7) cells in *T. tuberifera*, and the disc cells are smaller, 36–45 × 42–55 μm vs. 41–54 × 60–74 μm in *T. tuberifera*. Also, in *T. elegans* the leaf disc is rather low, 5–6 cells high vs. 6–9(10) cells in *T. tuberifera*. Its most notable features are the evenly thick-walled cells of the disc and the finely serrulate disc margins (Fig. 63: 1, 2). *Telaranea elegans* also typically lacks the conspicuous glaucous, water-repellent surface characteristic of *T. perfragilis* and *T. tuberifera*. Typically plants of *T. elegans* are only faintly glaucous, most evident in the youngest portions of the plant.

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in part. 13. First branch underleaf shown in fig. 12. 14. Antheridial stalk. (Figs. 1, 4–6, from type of *T. elegans*, WELT; 2, 3, from *Engel 17216*, Australia, New South Wales, Morton Natl. Park, Fitzroy Falls; 7–14, from type of *T. perfragilis*.)

Telaranea tuberifera J.J.Engel & R.M.Schust.

[Fig. 64; Fig. 67: 1, oil-bodies, p. 322]

Telaranea tuberifera J.J.Engel & R.M.Schust., Fieldiana, Bot. N.S. 14: 2. *f. 1.* 1983. Holotype: New Zealand, South Is., Fjordland Natl. Park, Falls Creek, Upper Hollyford River valley, along Milford Road, *Schuster 48775* (F).

Plants soft, flexuous, prostrate, often in interwoven, ± thick mats, glaucous, greenish white to ceraceous, becoming light brown with age, distinctly water-repellent; shoots medium, to 1 cm wide including branches. Branching loosely and somewhat irregularly pinnate, occasionally 2–3-pinnate, the branches of the *Frullania* type; branch half-leaf bifid, linear; first branch underleaf undivided, ciliate to subulate, inserted on ventral side of branch base, at times displaced toward the ventral-lateral side of the stem-branch juncture. Ventral-intercalary branches common, leafy or stoloniform and rooting in the substrate. Stems with cortical cells thin-walled, with a granular coating like that of the leaves, in 12–14 rows, those on ventral side of stem somewhat smaller, in section much larger than the numerous (ca. 25) medullary cells. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rigid, fragile (the lobe tips frequently caducous), spreading ± at right angles to stem, imbricate, plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion strongly incubous; leaves 595–770 μm wide × 775–840 μm long, subsymmetric, longer than broad, (3)4-lobed to 0.4–0.5, the lobes strictly parallel with disc margins, equal to or shorter than the disc. Lobes setaceous, typically 2 cells wide at extreme base (or rarely 4 cells wide, and then biseriate for 1[2] tiers), terminating in a uniseriate portion of (4)5–6(7) cells only weakly constricted at the septa; cells of uniseriate portion thin- to somewhat thick-walled, elongated, the walls not bulging. Disc ± symmetrically rectangular, often rather narrowly so, 6–9(10) cells high (from median sinus base to leaf base), 8–10(11) cells wide in distal portion, 8(11) cells wide at base; margins entire, the ventral ± straight, the dorsal curved (especially as seen *in situ*). Cells of disc in regular longitudinal rows, the cell walls thin to slightly thickened, trigones minute or absent; median disc cells large, short-rectangular to somewhat elongated, 41–54 μm wide × 60–74 μm long; basal row of disc cells considerably larger (much longer and generally a little wider) and forming an obvious tier; surface a dense granular and faintly striate coating. Oil-bodies present in all leaf cells, but disappearing in distal-most 1–2 cells of lobes, occupying small portion of cell, hyaline, 7–9 per median disc cell, irregular in shape, fusiform to long-linear to crescentic, often subvermiform, coarsely papillose. Underleaves much smaller than leaves, strongly spreading, distant, often gently curved dorsally, 3–4-lobed to 0.55–0.7, the lobes divergent, ciliiform, consisting solely of a uniseriate row of (2)3(4) elongated, thin-walled cells, the lobes terminating in a slime papilla; disc narrowed toward base, (2)3–4 rows of cells high and 8(9) cells wide, the basal tier of cells larger. Rhizoid initials in a band at base of underleaf lobes. Asexual reproduction by elliptic to ovoid tubers at the tips of stoloniform branches and probably by caducous leaf lobes.

Plants apparently dioecious. Androecia not seen. Gynoecia with bracts small for perianth size, those of innermost series concave, broadly ovate, ± regularly 4–6 ciliate-lobulate, the lobules 2(4) cells wide at base, with a uniseriate row of 2(3) cells, terminating in a slime papilla; lamina composed of ± regularly subrectangular cells, the margins each with 1–several weak teeth formed by the apical or free divergent end of marginal cells, terminating in a slime papilla, otherwise entire; bracteoles similar in form and size to bracts. Perianth long-emergent, fusiform, terete in basal and median sectors, the distal sector obscurely trigonous and with 3(4) plicae, the perianth narrowing toward the strongly contracted mouth; mouth cells thin-walled,

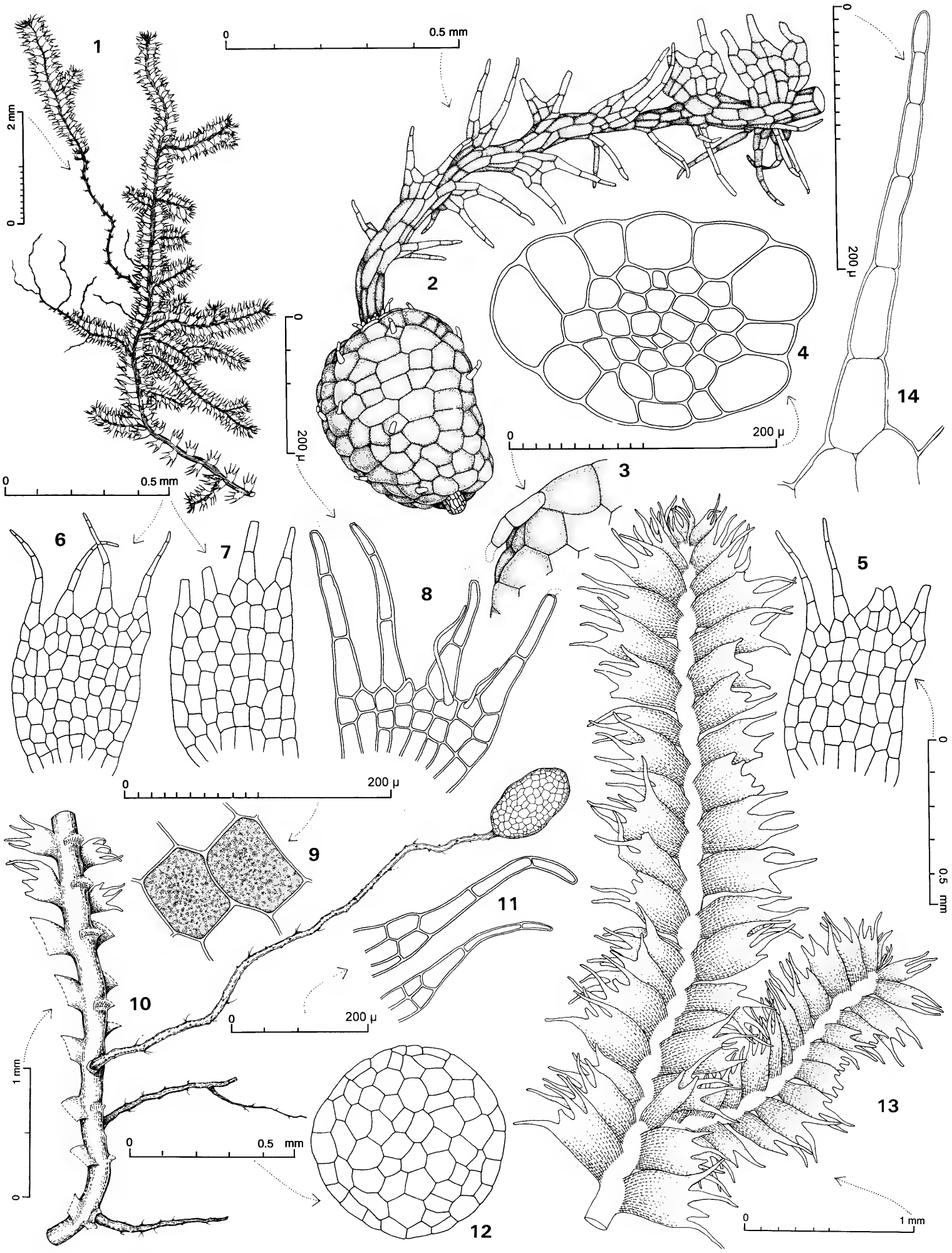

Fig. 64.
Telaranea tuberifera J.J.Engel & R.M.Schust. 1. Plant, dorsal view. 2. Germinating tuber; note scattered leaf rudiments and previous point of attachment of tuber to stolon at opposing end of tuber. 3. Portion of tuber surface showing a leaf rudiment. 4. Stem, cross section. 5–7. Leaves. 8. Underleaf; note rhizoid position. 9. Median discus cells showing surface detail in part. 10. Old, basal portion of shoot showing stoloniferous branches and a tuber. 11. First branch underleaves. 12. Tuber, cross section. 13. Portion of main shoot; note ragged leaf apices. 14. Median lobe of leaf. (All from type of *T. tuberifera*.)

often sinuate, partially or wholly laterally free, occasionally with a laterally free uniseriate row of 2 cells, the mouth thus shortly denticulate-subciliate; perianth 2–3-stratose in lower portion, the median portion 2-stratose.

Seta with 5–7 rows of outer cells surrounding an inner core of 9–17 much smaller cells. Capsule short-ellipsoidal, 476–497 μm wide, 910–980 μm long, the wall 24 μm thick, of 3 layers, the layers of ± equal thickness; outer layer of cells in tiers, rather regularly short-rectangular, with two-phase development, the longitudinal walls with well-defined sheet-like thickenings and nodule-like to spinose thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, local, non-pigmented to pigmented, nodular swellings), the transverse walls devoid of thickenings, or rarely with a few nodular swellings; innermost layer of cells ± tiered, irregularly narrowly rectangular, with semiannular bands common, rather narrow, close, usually complete, at times short and spinose, or rarely forked.

Spores 13.9–15.8 μm in diam., the wall yellow-brown, areolate (with a network of sharply defined furcate ridges that coalesce and delimit areolae). Elaters rigid, nontortuous, 8.2–10.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–4.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (0–80 m), South Island (10–930 m), North Island (0–890 m). Known from Fiordland, Westland, Canterbury (Arthur's Pass), Western Nelson, Southern North Island, Volcanic Plateau (Tauranga), Auckland (Kaimai Ra., Coromandel) and Northland (Waipoua) EPs. The species occurs mostly on Stewart Island and South Island and is infrequent and sporadic in the North Island. For the most part it is terricolous in lower- to middle- to upper-elevation forests of, for example, *Podocarpus*, or of *Nothofagus fusca*, *Dacrydium cupressinum*, *Weinmannia racemosa*, or of *N. menziesii* associated with *Dracophyllum* and *Quintinia serrata* or of dense, broadleaf forests of *Coprosma grandifolia*, *Ripogonum scandens*, *Rhopalostylis sapida* and ferns. It typically occupies very shaded niches in forests, where it may form pure, at times extensive colonies, often in sites too shaded for other plants. It is often found deep in shaded pockets or holes and on steep-sided banks, as, for example, under the lip-like overhang of the forest edge at the top of the bank of Waikohatu Stream. It is notable, for example, that *Hodgson 632* (Mt. Drury, a 20 m hill 1 km SE of Mt. Maunganui, Tauranga) was collected on the sides of a cave. It may be penalpine, where it may line deep pockets or deep crevices in ledges in scrub of, for example, *Olearia*, *Dracophyllum longifolium*, *Gaultheria* and *Ozothamnus leptophyllus*. It is found with *Mittenia plumula*, *Podomitrium phyllanthus*, *Psiloclada clandestina*, *Rhizogonium pennatum*, *Zoopsis argentea* and *Z. matawaia*.

The Butterfield Beach station on Stewart Island is of interest. Plants formed large sheets over a thin layer of sandy, loamy soil on bedrock near the mouth of a sea cave just a few meters above sea level on an exposed shoreline. The niche likely would be exposed to periodic salt spray (see Engel and Schuster, 1973).

Comments: This is the common New Zealand glaucous *Telaranea*, which has been known in the New Zealand literature as *T. centipes* (Hodgson, 1956; Allison and Child, 1975). *Telaranea centipes s. str.*, however, is confined to Tasmania, Victoria and New South Wales. The chief differences between *T. tuberifera* and *T. centipes* are in the shape of the disc, the disc margins and the form of the lobes. The lobes in *T. tuberifera* are setaceous and whisker-like (Fig. 64: 6, 13), composed of a uniseriate row of 5–6 cells, typically inserted on a base of 2 cells, which are a continuation of the highly regular longitudinal rows of cells of the disc (Fig. 64: 5, 7). The cells of the uniseriate row are elongated (to 4.6:1) and subcapillary (Fig. 64: 14).

They are much longer than those of *T. centipes* and are never bulging, nor are the lobes strongly constricted at the septa.

The leaf disc of *Telaranea tuberifera* is parallel-sided and the lobes strictly aligned with the disc margins as in *T. tetrapila* var. *roseana*, but *T. tuberifera* is distinctly glaucous, greenish white to ceraceous and almost tediously water-repellent, whereas *T. tetrapila* and its varieties are never so. As in *T. tetrapila* (p. 301), the disc cells of *T. tuberifera* are large and prominent, even under the dissecting microscope, but unlike *T. tetrapila*, the leaves are horizontally oriented, with the disc lying in essentially the same plane as the stem.

Telaranea perfragilis J.J.Engel & Merrill

[Fig. 63: 7–14]

Telaranea perfragilis J.J.Engel & Merrill, Fieldiana, Bot. 44: 72. *f. 20: 7–14*. 2004, *nom. nov. pro Telaranea fragilis* J.J.Engel & Merrill, Novon 9: 341. *f. 2*. 1999, *non T. fragilis* Mizut., J. Hattori Bot. Lab. 40: 449. *f. 1*. 1976 (Philippines). Holotype: New Zealand, North Is., North Auckland Prov., NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20465* (F); isotype: (CHR).

Plants delicate, flexuous, prostrate in thin straggling mats or as isolated strands among other bryophytes, glaucous, whitish to bluish green, dull and distinctly water-repellent; shoots medium, to ca. 1 cm wide, including branches. Branching loosely and irregularly 1-pinnate, the branches of the *Frullania* type; branch half-leaf bifid, linear; first branch underleaf undivided, subulate, inserted on the ventral side of branch at branch base. Ventral-intercalary branches present, both leafy and stoloniform. Stems dorsiventrally flattened, with cortical cells distinctly differentiated, in 9–12 rows, thin-walled, the dorsal cortical cells much larger than medullary cells; medullary cells ca. 16. Rhizoids issuing from distal tier of underleaf disc cells. Leaves fragile, typically erose-truncate (the lobes all or mostly broken off and often the distal tiers of disc cells missing), widely spreading, at times nearly at right angles to stem, distant to loosely imbricate, plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion distinctly incubous; leaves 260–290 μm wide, the fragmented leaf 280–390 μm long (including basal cell of lobe), 465–505 μm long with lobes, leaves subsymmetric, 4-lobed to ca. 0.4, the lobes ± parallel with disc margins or only slightly divergent, shorter than the disc. Lobes (when present) subcaudate, 2 cells broad at base, terminating in a uniseriate row of 6–7 cells, distinctly constricted at the septa (especially in basal portion); lobe cells thin-walled, the basal pair of lobe cells and the basal cell of uniseriate row barrel-shaped and bulging. Disc ± symmetrically quadrate to subrectangular, 5–6(7) cells long (from median sinus base to leaf base), mostly 8 cells wide throughout; margins about equal in length, distinctly crenulate due to bulging marginal cells, ± straight to weakly arched. Cells of disc in regular longitudinal rows, thin-walled but firm or moderately thick-walled, trigones minute or absent; median disc cells large, subquadrate, 33–45 μm wide × 40–52 μm long, the basal row somewhat longer, forming an obvious tier; surface with a finely granular and faintly striate coating. Underleaves much smaller than leaves, widely spreading, distant, often gently curved dorsally, 4-lobed to 0.75–0.85, the lobes widely divergent, ciliiform, consisting of a uniseriate row of 3–4 elongated, thin-walled cells, inserted on 2 disc cells, terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide. Asexual reproduction evidently by fragmentation of leaf lobes and disc.

Plants apparently dioecious. Androecia on short, abbreviated, ventral-intercalary branches lacking normal vegetative leaves; bracts rather closely imbricate, strongly dorsally assurgent, deeply concave, 2–3-lobed, each lobe terminating in a uniseriate row of (2)3 moderately elongated, thick-walled cells; lamina margins irregularly minutely crenulate by few cells with the free margin bulging, otherwise with a few slime papillae; bracts monandrous; antheridia large for bract size, the stalk biseriate; bracteolar antheridia absent. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: North Island (95–820 m). Known from Southern North Island (Ruamahanga Valley), Gisborne (Pongakawa River), Auckland (Auckland City, Coromandel Peninsula) and Northland (Waipoua) EPs. The species occurs on moist, clayey banks or at times over rock in forests. The type occurred on a vertical clayey bank above a small stream in an old *Kunzea* forest with *Agathis australis* and *Phyllocladus trichomanoides*.

Comments: Plants of this species are delicate and fragile; in shoots freshly mounted in water the leaves often can be observed breaking apart (Fig. 63: 10, arrow), and it is likely that detached lobe and disc cells function as gemmae. Hodgson (1956) cited populations referable to this species and included them under her treatment of *Lepidozia centipes*. *Telaranea perfragilis* resembles *T. centipes* in the conspicuously turgid, bulging cells of the disc margins and lobes, but the leaves are 4-lobed in *T. perfragilis* and the disc is typically parallel-sided and 8 cells wide throughout (Fig. 63: 7). In *T. centipes* the disc is cuneate and up to 15 cells wide in the distal portion and the leaves are sometimes 5–6(7)-lobed on robust main shoots. In addition, the basal cells of the uniseriate row in *T. perfragilis* are fat and bulging, but the distal portion of the uniseriate row, when present, is slenderly tapering, with narrower, more elongate cells (Fig. 63: 8).

Sect. ***Tricholepidozia*** (R.M.Schust.) J.J.Engel & Merrill

Telaranea sect. *Tricholepidozia* (R.M.Schust.) J.J.Engel & Merrill, Fieldiana, Bot. 44: 73. 2004.
Telaranea subg. *Tricholepidozia* R.M.Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: *Telaranea pulcherrima* var. *mooreana* (Steph.) J.J.Engel & Merrill (≡ *Lepidozia mooreana* Steph.)

Telaranea remotifolia E.A.Hodgs.

[Fig. 65; Fig. 67: 2, 3, oil-bodies, p. 322]

Telaranea remotifolia E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. *Lepidozia remotifolia* E.A.Hodgs., Trans. Roy. Soc. New Zealand 83: 603. *pl. 2, f. 14*. 1956, *non L. remotifolia* Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, 2: 202. 1934 (Taiwan). Type: New Zealand, North Is., Tararuas, Ruamahanga Valley, 3 Dec. 1933, *Zotov 9275* (MPN!); isotype: (CHR!).

Plants soft, appearing etiolated and often rather flaccid, loosely prostrate and straggling, in pure, intermingled loose mats or as isolated wisps among other bryophytes, pale green to grass-green, the plants when dry glass-like, the stems sinuous and the leaves shrunken and inconspicuous; plants stenotypic in stature, small, to 1.2 cm wide, including branches. Branching very irregularly and distantly pinnate, the branches of the *Frullania* type, typically long, weak and filiform; branch half-leaf undivided and subulate or bifid and narrowly rectangular; first branch underleaf asymmetrically bifid, the dorsal lobe leaf-lobe-like, the ventral lobe shorter

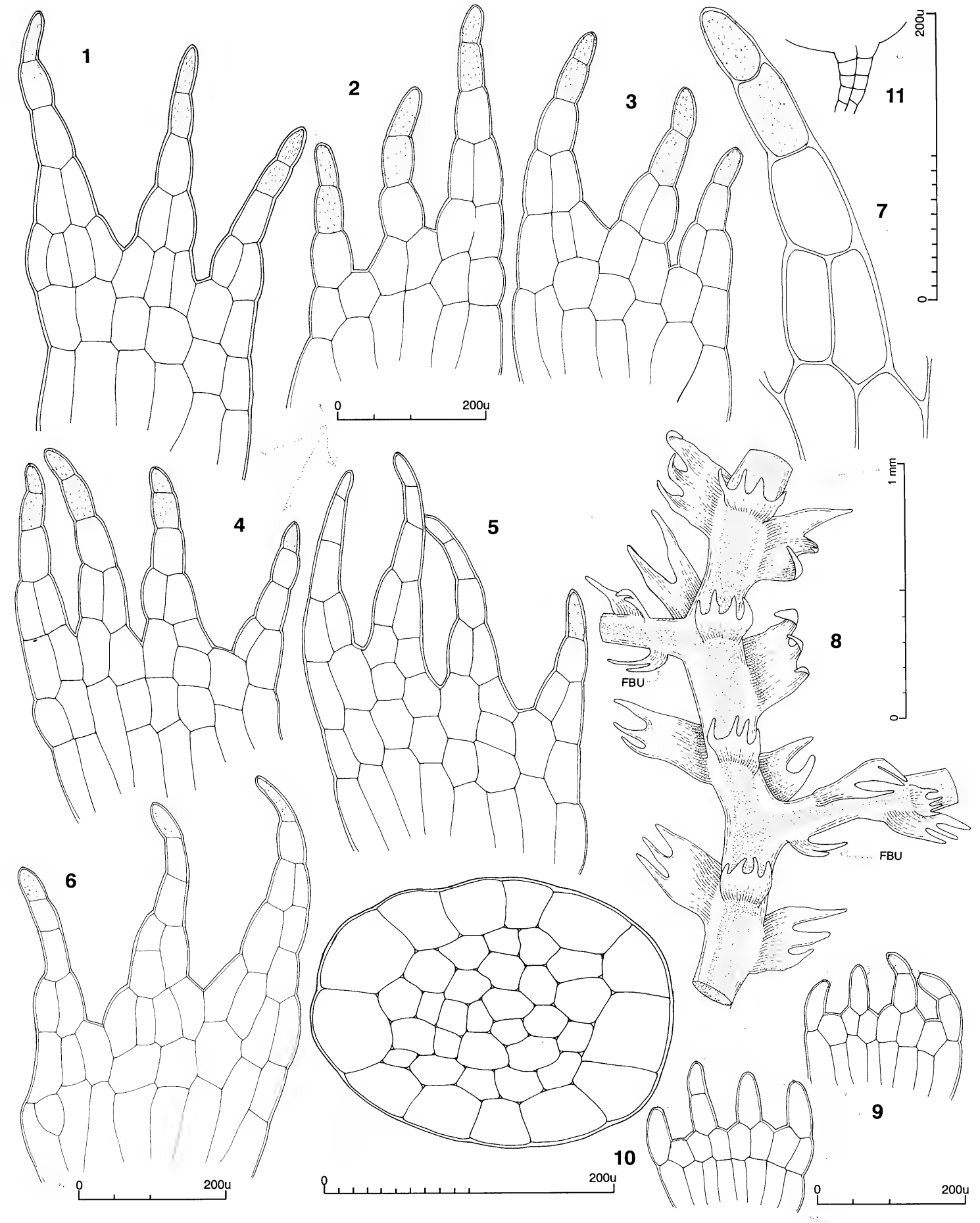

Fig. 65.
Telaranea remotifolia E.A.Hodgs. 1–6. Leaves, cellular detail. 7. Dorsal lobe of leaf. 8. Main shoot (FBU = first branch underleaf), the medullary strand shown with stipple; ventral view. 9. Underleaves, cellular detail. 10. Stem, cross section. 11. Antheridial stalk. (Figs. 1, 5, 6, 10, from *Engel 18921*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, Blue R.; 2–4, 7–9, from type; 11, from *Child 5366*, New Zealand, South Is., Western Nelson EP, 5 km N of Runanga.)

and terminating in a slime papilla, the first branch underleaf inserted on ventral to ventral-lateral side of branch near juncture of branch and main axis. Ventral-intercalary branches rare, leafy. Stems often appearing fleshy and large for plant size, with cortical cells in 10–13 rows, distinctly differentiated, thin-walled, in section much larger than the numerous (17–25[34]) medullary cells, the medullary strand distinctly visible in surface view of stem. Rhizoids not seen. Leaves on main shoot delicate, brittle, obliquely to widely spreading, conspicuously remote and alternately arranged, weakly convex, the insertion distinctly incubous to almost longitudinal; leaves 265–385 μm wide × 440–565 μm long, asymmetric, 3–4-lobed to ca. 0.55, the lobes about equal to disc or a little longer. Lobes narrowly attenuate, 2–4 cells wide at extreme base, terminating in a uniseriate row of 2–3(4) cells, the dorsal lobe(s) typically somewhat stronger and with 1(2) biseriate tiers between the uniseriate portion and the extreme base, the ventral lobe typically weaker; cells of the uniseriate portion somewhat elongate, thin-walled, the septa neither thickened nor swollen; surface of lobe tips finely striate-papillose, otherwise smooth. Disc somewhat asymmetric, parallel-sided to weakly cuneate, 2–3(4) cells high (from median sinus base to leaf base), 6–11 cells wide in distal portion narrowing to 6–8 cells wide in basal portion. Cells of disc thin-walled, trigones lacking, the basal tier of disc cells at times considerably longer (particularly when disc is 2 cells high), the distal tier(s) shorter, ± elongated, (35)42–53 μm wide × 72–90 μm long; surface smooth. Oil-bodies hyaline, coarsely papillose, the spherules somewhat protruding beyond membrane, the median disc cells with 6 oil-bodies per cell, globose to subglobose and 5–5.9 μm in diam., the cells at sinus base with 5–6 oil-bodies per cell, elliptic to subfusiform, 5.3–6.4 × 9.5–12.2 μm, a few ca. 6.4 × 14.2 μm. Underleaves much smaller than leaves, roughly equal in width to the medullary strand of the stem, spreading, distant, slightly convex (ventral view), 3–4-lobed to 0.45–0.55, the lobes consisting of a uniseriate portion of 1–2(3) somewhat elongated cells, terminating in an elongate slime papilla and a base of 2 laterally juxtaposed cells; disc rectangular (broader than high) to weakly cuneate, 2 cells high (median sinus), 6–8 cells wide in distal and basal portions. Asexual reproduction lacking.

Plants dioecious. Androecia delicate and easily detached, either on short primary *Frullania*-type branches with a few cycles of normal vegetative leaves prior to androecial formation, or on short, abbreviated, ventral-intercalary branches from leading shoots, the androecium exceptionally long for genus, with up to 9 pairs of bracts; bracts closely to rather loosely imbricate, dorsally assurgent, deeply concave, bilobed to ca. 0.5, the lobes acuminate and terminating in a single cell or a uniseriate row of 2 cells, the tip cell of the lobe rather elongated (to 84 μm long, to 3.2:1); dorsal margin somewhat dilated and with a large tooth/lobule with its free margin crenulate, at times with a slime papilla; ventral margin with a conspicuous tooth; bracts monandrous; antheridial stalk biseriate; bracteolar antheridia absent. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (20–30 m), South Island (25–915 m), North Island (95–425 m), Chatham Islands (80 m). Known from Fiordland, Otago, Westland, Western Nelson, Taranaki, Auckland and Northland EPs.

Sporadically occurring throughout its range, the species seems to have a rather broad ecological amplitude, at least with respect to elevation. For example, on Stewart Island (Fern Gully Track, 20–30 m) the species was found on very old wood of a long-abandoned bridge in dense shade of a forest with a *Fuchsia excorticata – Griselinia littoralis* canopy with a *Blechnum discolor* ground tier. Yet it occurs above treeline on stream banks and submerged boulders as well as over peaty soil in shallow pools at bog edges with abundant *Sphagnum* (Lake Shirley, Fiordland, 915 m), and in an area of tussock grassland with a mosaic of scattered

bogs and patches of *Dracophyllum*, *Halocarpus bidwillii*, *Hebe* and *Donatia* (summit of Mt. Maungatua, 30 km W of Dunedin, 825 m). The species also occurs in mixed *Nothofagus* forests (Blue River, S of Haast Pass, 310 m), as well as in dense *Nothofagus* forests of the southern portion of South Island, where it is terrestrial or on rotted logs, occurring at times with *Acromastigum cunninghamii*, *Telaranea tuberifera* and *Lepidozia kirkii*. In the Borland Burn it occurred abundantly in dense cushions on a stream bank under *Nothofagus solandri* forest, with *Balantiopsis tumida*, *Pachyschistochila subhyalina* and *Schistochila balfouriana*. Along the Aongatete River (Kaimai Ra., 425 m) it has been found over thin soil on vertical bed rock in *Dacrydium cupressinum – Beilschmiedia tawa* forest with a *Cyathea* understory. Within the steep-sided valley of Waikohatu Stream (Waipoua Forest, 290 m) it occurs in *Agathis australis* forests with *Weinmannia silvicola* over soil of streambed rocks or of stream banks.

Comments: *Telaranea remotifolia* has a lax, etiolated aspect when dry. The pale green, loosely matted stems appear fleshy and out of proportion to the leaves, which are distant, shrunken, distinctly glass-like and strongly convex. The leaf lobes are often sharply decurved and claw-like. Another of our species with a similar lax, etiolated appearance is *T. nivicola*, but this has a greatly reduced disc, consisting only of the partially united paired basal cells of the leaf lobes.

Optimally developed shoots have the aspect of an etiolated *Telaranea tetrapila*. Leaves on such shoots are frequently 4-lobed, the disc is 3–4 cells high (Fig. 65: 1, 4, 5), and the lobes biseriate, at least in part (Fig. 65: 4, 5). The leaves of somewhat weaker shoots have a disc 2–3 cells high and are mostly 3-lobed (Fig. 65: 2). In all cases, however, the ventral leaf lobe is the smallest. Also distinctive are the underleaves, which are particularly small and are about equal in width to the medullary strand of the stem (Fig. 65: 8), which is clearly visible through the cells of the hyaloderm.

Plants with abbreviated leaf discs (2 cells high) could be confused with *Telaranea tetradactyla*, which also has a rather glass-like appearance, but even when suboptimal, the transverse leaf insertion of this species will distinguish it from *T. remotifolia*.

Telaranea pulcherrima (Steph.) R.M.Schust.

[Fig. 66; Fig. 67: 4, oil-bodies, p. 322]

Lepidozia pulcherrima Steph., Sp. Hepat. 3: 600. 1909. *Telaranea pulcherrima* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: New Zealand, Okarito, *Kirk 588* (G!, CHR 4844!).

Plants subisophyllous, with a soft and woolly appearance, flexuous, prostrate, superficially appearing like *Trichocolea mollissima*, markedly pale green, distinctly nitid when dry; shoots medium, to 1.3 cm wide (including branches). Branching regularly and rather densely 1-pinnate, 2-pinnate in broadest portion of plant, the branches of the *Frullania* type; branch half-leaf 4–5(6)-lobed, cuneate, the lobes diverging; first branch underleaf 3–4-lobed, inserted on ventral-lateral side of juncture of branch and main shoot. Ventral-intercalary branches frequent, leafy, often becoming leading shoots. Stems with cortical cells poorly differentiated, in 24–30 rows of thin-walled cells, the dorsal and lateral somewhat larger than the exceedingly thin-walled medullary cells but hardly forming a differentiated hyaloderm, the 6–8 or more ventral cortical cells not or scarcely larger than medullary cells; medullary cells numerous (ca. 75), thin-walled. Rhizoids originating from basal tier of underleaf cells. Leaves soft yet firmly attached, the disc spreading, the lobes becoming suberect, the leaves closely imbricate, feebly

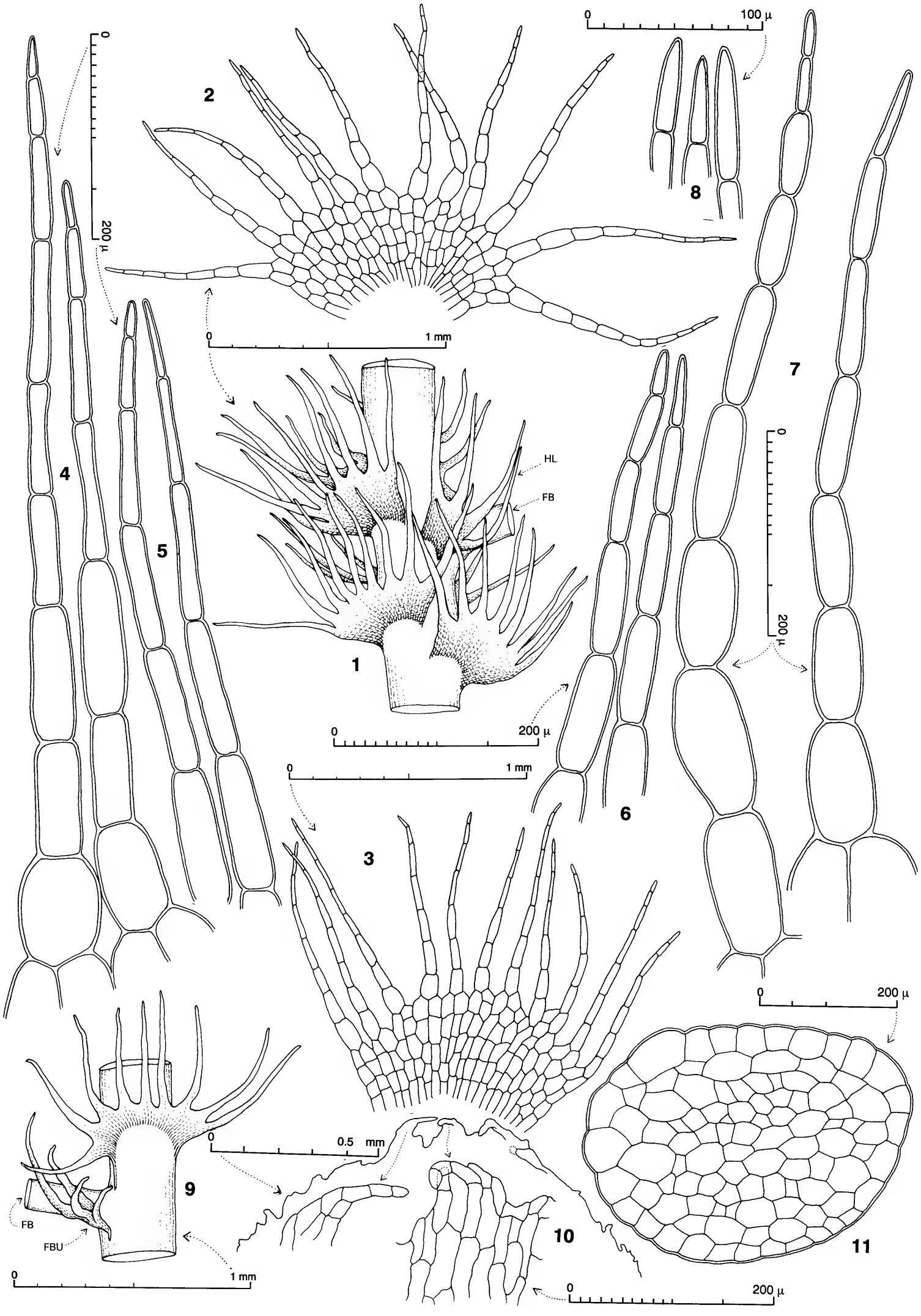

Fig. 66.
Telaranea pulcherrima (Steph.) R.M.Schust. (figs. 1, 2, 6, 7, 9, var. *pulcherrima*; 3–5, 8, 10, 11, var. *mooreana* (Steph.) J.J.Engel & Merrill). 1. Sector of main shoot, dorsal view (FB = *Frullania*-type branch; HL = half-leaf). 2, 3. Leaves. 4–7. Leaf lobes. 8. Terminal cells of leaf lobes. 9.

convex due to slight decurving of lobes, the insertion subtransverse to weakly incubous; leaves 1015–1825 μm wide × 1015–1400 μm long, very slightly asymmetric, ± equally (7)9–12(13)-lobed to 0.55–0.65, the lobes ± symmetrically spreading, longer than the disc. Lobes ciliiform, widely spreading, uniseriate throughout, inserted on a triangular base composed of 2 disc cells, the uniseriate portion 6–9(10) cells long, the cells ± thin-walled, the septa somewhat thickened in the corners, moderately to distinctly constricted, the basal cell 40–66 μm wide × (110)120–140 μm long (1.7–3.3:1), the longest cells 86–130(160) μm long and 3.6–5.5(6.3):1 in var. *pulcherrima*, 125–160 μm long and 7.4–9.6:1 in var. *mooreana*, terminal cell shorter than penultimate cell, rather sharply tapering to a point. Disc ± symmetrically to slightly asymmetrically short-cuneate, 4–5 cells high in dorsal sector (including intermediate cells and paired cells at bases of lobes), 3–4 cells high in ventral sector, 18–20(24) cells broad at midpoint of disc. Cells of disc in ± regular tiers, thin-walled but not delicate, without trigones, the median disc cells large, 38–48 μm wide × 62–84 μm long; basal row of disc cells (intermediate cells) narrower; surface smooth. Oil-bodies in all cells of leaf ?except terminal cell of uniseriate row, occupying a very small portion of cell, hyaline, 5–8 per disc cell, moderately papillose, the spherules somewhat protruding beyond the membrane, the oil-bodies elliptic to more often fusiform to subcrescentic. Underleaves similar to leaves, the disc spreading to subsquarrose (the lobes erect), imbricate, symmetrically 6–10-lobed to 0.8, the lobes symmetrically spreading; disc short-cuneate, 4–5(6) cells high (median sinus), (15)19–23 cells broad in median portion, the cells in ± regular tiers; surface as in leaves. Asexual reproduction lacking.

Dioecious. Androecia either terminal on short, secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary subspicate branches; bracts rather closely imbricate, strongly dorsally assurgent, 3-lobed, the dorsal somewhat inflexed (and ± oriented toward shoot apex), the lobes 3–4 cells wide at base, terminating in a uniseriate row of 3–4 elongate cells; lamina with dorsal margin somewhat incurved to form a weak pocket, with a few slime papillae or small teeth (one at times large, lobuliform and inflexed); bracts monandrous; antheridial stalk biseriate; bracteolar antheridia absent. Gynoecia with bracts very small for perianth size, those of innermost series strongly concave and ± abruptly involute-tubular forming a subcucullate apex, the bracts broadly elliptic to broadly obovate; apices very shallowly and irregularly 3–4-lobulate, the lobules composed of cells similar to those of lamina, terminating in a short uniseriate cilium of 2–3 elongated cells, often with a terminal slime papilla; lamina composed of ± regularly subrectangular cells, the margins curved, the marginal cells obliquely oriented and sinuous, the free apical ends diverging and forming irregular denticulations, with slime papillae frequent; bracteoles similar in form to bracts but slightly smaller. Perianth large for plant size, terete for most of its length, trigonous and 3-plicate only near the summit, the perianth gradually tapering toward the mouth; mouth crenate-denticulate by the variably projecting, bluntly rounded, marginal cells.

Capsule (Schuster, 1969c, p. 33; 2000a, fig. 81) wall 5-stratose, the outer layer ± equal in thickness to intermediate layers; outer layer of cells in tiers, with primary cells subdivided by

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Sector of main shoot, ventral view (FB = *Frullania*-type branch; FBU = first branch underleaf). 10. Apex of innermost ♀ bract, with (at arrows) 2 lobules shown in detail. 11. Stem, cross section. (Figs. 1, 6, 9, from *Engel 21771*, New Zealand, South Is., Westland EP, ca. 4 km N of Haast R.; 2, 7, from type of *Lepidozia pulcherrima*; 3, 4, 8, from type of *Lepidozia mooreana*; 10, 11, from *Engel E16407*, Tasmania, road between Zeehan and Trial Harbour; 5, from *Engel E19927*; Tasmania, Tahune Forest Reserve, along Huon R.)

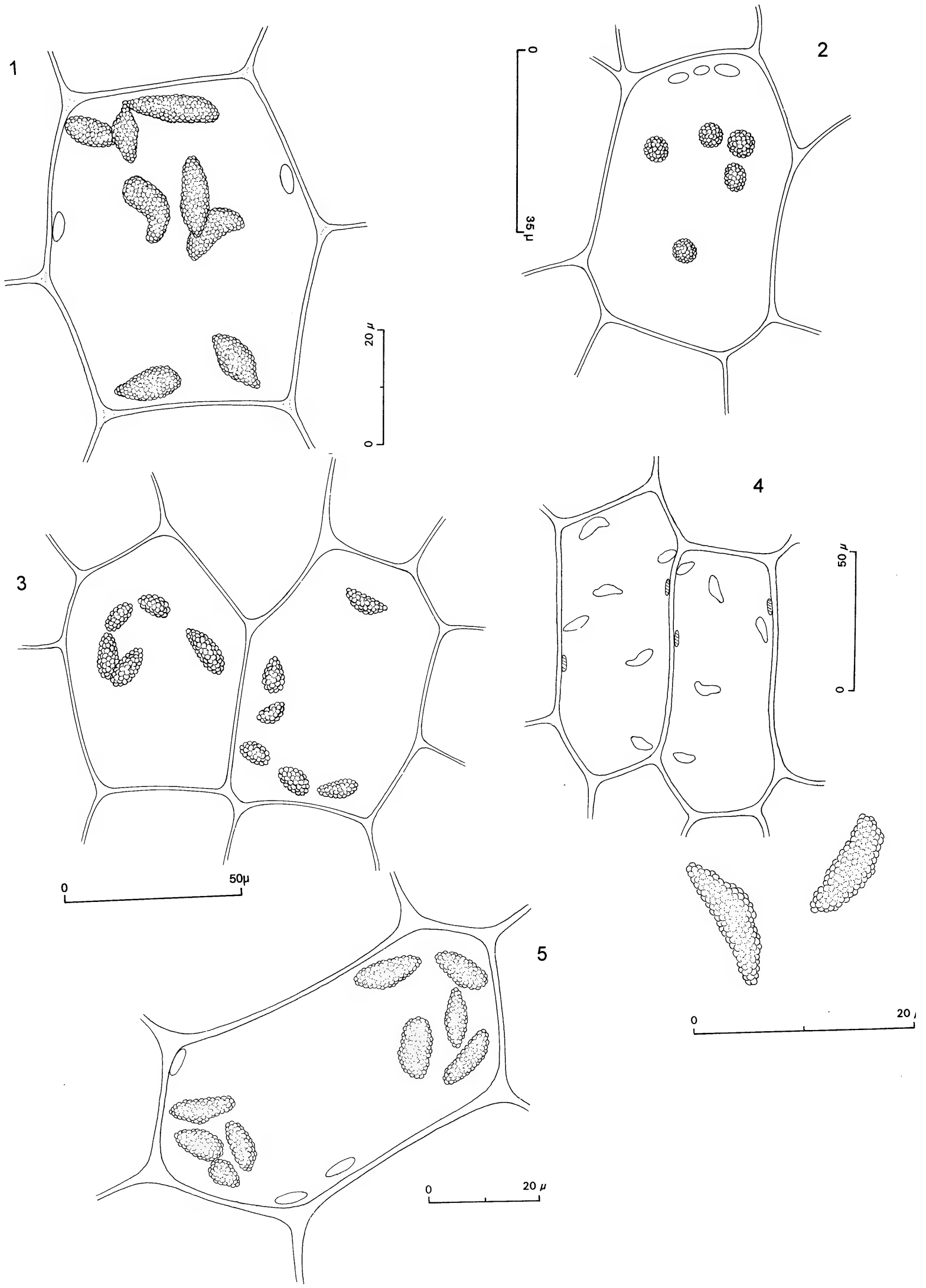

Fig. 67.
Oil-bodies, all (except fig. 3) with the outline of a few chloroplasts included. 1. *Telaranea tuberifera* J.J.Engel & R.M.Schust. Median disc cell. 2. *Telaranea remotifolia* E.A.Hodgs. Median cells

3 longitudinal walls with sheet-like sinuous thickenings, the transverse walls devoid of thickenings; innermost layer of cells ± tiered, narrowly rectangular, with semiannular bands common, mostly complete.

Spores areolate. Elaters rigid, not or weakly tortuous, 8.6–10.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 4.3 μm wide.

Distribution and Ecology: New Zealand: Stewart Island (100–475 m), South Island (0–900 m); Australia: Tasmania (common), Victoria (rare). In New Zealand known from Fiordland (Supper Cove, Borland Burn), Southland (Awarua Bay), Westland (Haast, Mikonui River) and Western Nelson (Stockton Plateau) EPs.

In our area of sporadic distribution from Southland to Nelson; it is apparently somewhat frequent on Stewart Island, and is common in streambeds on Stockton Plateau. This species forms pure, translucent, light yellow-green to whitish green mats in very wet sites. It is associated with quiet pools and small, quiet rills or narrow creek systems where it occurs within the pools or loosely over very deep humus or sand or silt at the creek margins. The humidity is always very high in such sites, which, on Stewart Island, are in the shade of podocarp–hardwood forests of *Dacrydium cupressinum* and *Weinmannia racemosa*, with a subcanopy of *Dicksonia squarrosa* and *Ripogonum scandens* or of stunted and dense *Leptospermum scoparium – Dracophyllum – Weinmannia* forest 3–4 m tall. In the Haast River area the plant occurs at sea level in open swampy areas with *Sphagnum* and scattered *Leptospermum scoparium* in low areas between hummocks. At Truran Saddle (Mikonui River, Westland, 500 m) it is found under *Weinmannia racemosa* forest on very wet peat and tree roots, with *Riccardia crassa*. On Stockton Plateau, it is common along small stream margins, usually in silt or sand flood-deposited on soil banks or rocks. Among the most hygrophytic of the *Telaranea* species, usually confined to sites (damp rocks near water, perhaps subject to inundation, and peaty ground where submersion could occur) where never subject to drying out.

Comments: The pale yellowish green, soft-textured, rather spongy, regularly 2(3)-pinnate, plumose shoots, and the multiple leaf lobes, radiating fan-like from the disc (Fig. 66: 1–3) will immediately distinguish this species. In all these respects, the plants have the aspect of a small, delicate *Trichocolea*.

Two varieties of the species are recognized, one in New Zealand, the other, var. *mooreana* (Steph.) J.J.Engel & Merrill, in Tasmania and Victoria.

Telaranea pulcherrima (Steph.) R.M.Schust. var. ***pulcherrima***

[Fig. 66: 1, 2, 6, 7, 9]

Longest cells in distal portion of lobes shorter than in var. *mooreana*, 86–130(160) μm long, 3.6–5.5(6.3):1 (see Fig. 66: 6, 7).

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of disc. 3. *Telaranea remotifolia* E.A.Hodgs. Cells at base of median sinus. 4. *Telaranea pulcherrima* (Steph.) R.M.Schust. Disc cells, below 2 oil-bodies at higher magnification. 5. *Telaranea tetrapila* (Taylor) J.J.Engel & Merrill var. *tetrapila*. Disc cell. (Fig. 1, from *Glenny 9144*, New Zealand, South Is., Westland EP, Mt. Turiwhate, near summit; 2, 3, from *Engel 24055*, New Zealand, Stewart Is., Rakiura Natl. Park, Fern Gully Track; 4, from *Glenny 9513*, New Zealand, South Is., Western Nelson EP, Mt. Augustus; 5, from *Glenny 9237*, New Zealand, South Is., Western Nelson EP, Arthur Ra., Pages Saddle.)

Sect. ***Transversae*** J.J.Engel & Merrill

Telaranea sect. *Transversae* J.J.Engel & Merrill, Phytologia 79: 251. 1996 (1995). Type: *Lepidozia lindenbergii* Gottsche.

Lepidozia sect. *Capillares* Gottsche, Lindenb. & Nees, Syn. Hepat. 211. 1845, "IV. *Capillares*." Lectotype (*fide* Engel and Merrill, 2004): *Lepidozia lindenbergii* Gottsche, *non Telaranea* sect. *Capillares* J.J.Engel & Merrill, Phytologia 79: 251. 1996 (1995).

Kurzia subg. *Leucolepidozia* R.M.Schust., J. Hattori Bot. Lab. 48: 356. 1980. Type: *Kurzia quadriseta* Grolle.

Telaranea lindenbergii (Gottsche) J.J.Engel & Merrill

[Fig. 68: 1–8, 11, 13–16; Fig. 69; Fig. 77: 1, oil-bodies, p. 355]

Lepidozia lindenbergii Gottsche *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 213. 1845. *Mastigophora lindenbergii* (Gottsche) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Telaranea lindenbergii* (Gottsche) J.J.Engel & Merrill, Phytologia 79: 252. June 1996 (1995). Type: "Nova Zeelandia inter *L. praenitentem* (Hb. Hk.)" (W!, Lindenberg Hepat. no. 4849).

For synonymy, see under varieties.

Plants delicate, often with a bristly appearance, soft, flexuous yet firm (straight and ± wiry in var. *mellea*), prostrate, pale green to pale yellow-green (or brownish yellow to rust-brown in var. *mellea*), nitid when dry; plants small, to 5 mm wide, including branches. Branching rather regularly 1–2-pinnate, at times ± plumose, the branches rather closely spaced, terete (complanate-foliate in var. *complanata*), scarcely tapering (long-flagelliform in var. *mellea*); branch leaves transversely inserted (incubous in var. *complanata* and var. *papillata*); branch half-leaf 2-lobed; first branch underleaf undivided and ciliiform, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, leafy. Stems flexuous, often appearing stout for plant size; cortical cells distinctly differentiated, somewhat thick-walled; cortical cells in section much larger than the numerous (ca. 40–67) medullary cells. Rhizoids often copiously produced from cells of underleaf disc. Leaves on main shoot rigid, widely spreading to squarrose, rather distant on main stems to closely imbricate on the branches, plane or somewhat hand-like due to incurving of lobes, typically transversely inserted and oriented (at times weakly incubous), transverse or weakly incubous on branches; leaves 245–280 μm wide × 175–225 μm long ranging to 390–440 μm wide × 235–320 μm long (4-lobed) to 525–735 μm wide × 370–460 μm long (6-lobed), symmetric to weakly asymmetric, 4–6(7)-lobed to 0.65–0.8, the lobes divergent, longer than disc height. Lobes ciliiform, typically uniseriate to the base, inserted on a triangular base composed of 2 disc cells (or sporadically with an additional biseriate tier between base and uniseriate row), the uniseriate portion 5–6(7) cells long (4–5 cells long in var. *papillata*), with cells moderately thick-walled and firm, straight-sided and without or with weakly bulging septa; surface smooth. Disc semicircular, 2 cells high (locally 3, exceptionally 4 in var. *mellea*) (from median sinus base to leaf base) including paired cells at bases of lobes, the basal tier of cells elongate and 8 cells wide in 4-lobed leaves to 12 cells wide in 6-lobed leaves. Cells of disc somewhat thinner-walled than lobe cells but firm, trigones lacking, the largest cells (in median sector of disc) 17–24 μm wide × 40–60 μm long (basal tier); basal tier of disc cells often longitudinally elongated; surface smooth. Oil-bodies in all cells of leaf (?distal 2 cells of lobe excepted), occupying a moderate portion of cell lumen, pale smokey grey, opaque, 7–9 per disc cell, finely papillose, globose to rather broadly elliptic to subfusiform, 3.8–4.8 × 7.2–9.6 μm. Chloroplasts very narrow seen edge on. Underleaves much smaller than leaves, inconspicu-

ous, 4–5-lobed nearly to base, the lobes ciliiform, the uniseriate portion formed of 3–4 somewhat elongated cells, terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide (in 4-lobed underleaves). Rhizoid initial cells small, subquadrate, formed from some or all cells of underleaf disc.

Plants dioecious. Androecia either terminal on short to moderately long primary or secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary, spicate branches; bracts closely imbricate, strongly dorsally assurgent, deeply concave-subcucullate, 2(3)-lobed to ca. 0.5, the lobes subcaudate, terminating in a uniseriate row of 3–4 rather elongated, moderately thick-walled cells, the terminal cell tapering to summit, to 3:1; dorsal margin of lamina somewhat dilated and incurved, crenulate and with a few slime papillae or with a 1–several-celled, often sharp tooth; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent. Gynoecia with bracts small for perianth size, those of innermost series concave, short-oblong to ovate; apices shallowly (3)4-lobulate, the median sinus a little deeper, the lobules acuminate, terminating in a uniseriate cilium of 2–4 somewhat elongated cells, often with a terminal slime papilla; lamina composed of ± regularly subrectangular cells, the margins curved, with a few blunt teeth formed by the divergent apical or free end of marginal cells, or margins subentire or with a few small 1–2-celled teeth; bracteoles similar in form to bracts, but 0.5–0.75 their size. Perianth long-emergent, terete in basal sector, trigonous above, basically 3-plicate but with several accessory smaller plicae, the perianth narrowing toward the contracted mouth; mouth with 9–13 caudate lobes, the lobes each with a base composed of 2–4 laterally juxtaposed, elongate cells, the lateral cells of base often with the distal end protruding to form a "shoulder," the lobes each terminating in a flexuous or stiff setose cilium composed of a uniseriate row of 3–5 elongate, rather thick-walled cells, the basal 1–2 cells 13–20 μm wide × 96–130 μm long (5.7–8.3:1) (var. *lindenbergii*), or 14–22 μm wide × 60–90 μm long (3.1–4.6:1) (var. *complanata*); perianth 2-stratose in basal portion, the cells in section radially elongate.

Seta with 8 rows of outer cells, surrounding an inner core of 15–18 much smaller cells. Capsule short-ellipsoidal, 553–616 μm wide, 1120–1295 μm long, the outer wall undulate in transverse section, the primary walls shorter than the thickened secondary walls, alternatively 29–31 μm to 38–41 μm thick, of 3 layers, the outer layer at its thickest point equivalent to the combined thickness of the two inner layers; outer layer of cells (surface view) in tiers, thin-walled, rather regularly short-rectangular, with two-phase development, the longitudinal walls with rather weakly developed nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings, the transverse walls also devoid of thickenings; innermost layer of cells ± tiered, somewhat irregularly narrowly rectangular, with semiannular bands common, rather narrow, close, usually complete, sporadically forked and anastomosing to delimit fenestrae.

Spores 13.4–14.9(15.4) μm in diam., the wall pale brown, with a network of low but sharply defined papillae and short-vermiculate markings that coalesce and delimit areolae. Elaters rigid, ± sinuous, 7.7–9.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.8–4.8 μm wide.

Comments: This common and widespread species was treated by Hodgson (1956) as a synonym of *Telaranea tetradactyla*. The name *Lepidozia lindenbergii* has been used extensively for the New Zealand plant. All of the published species in this complex have proved to be *T. lindenbergii*, whereas *T. tetradactyla s. str.* (p. 336) has no synonyms. For a discussion of the differences between these two species see under *T. tetradactyla*.

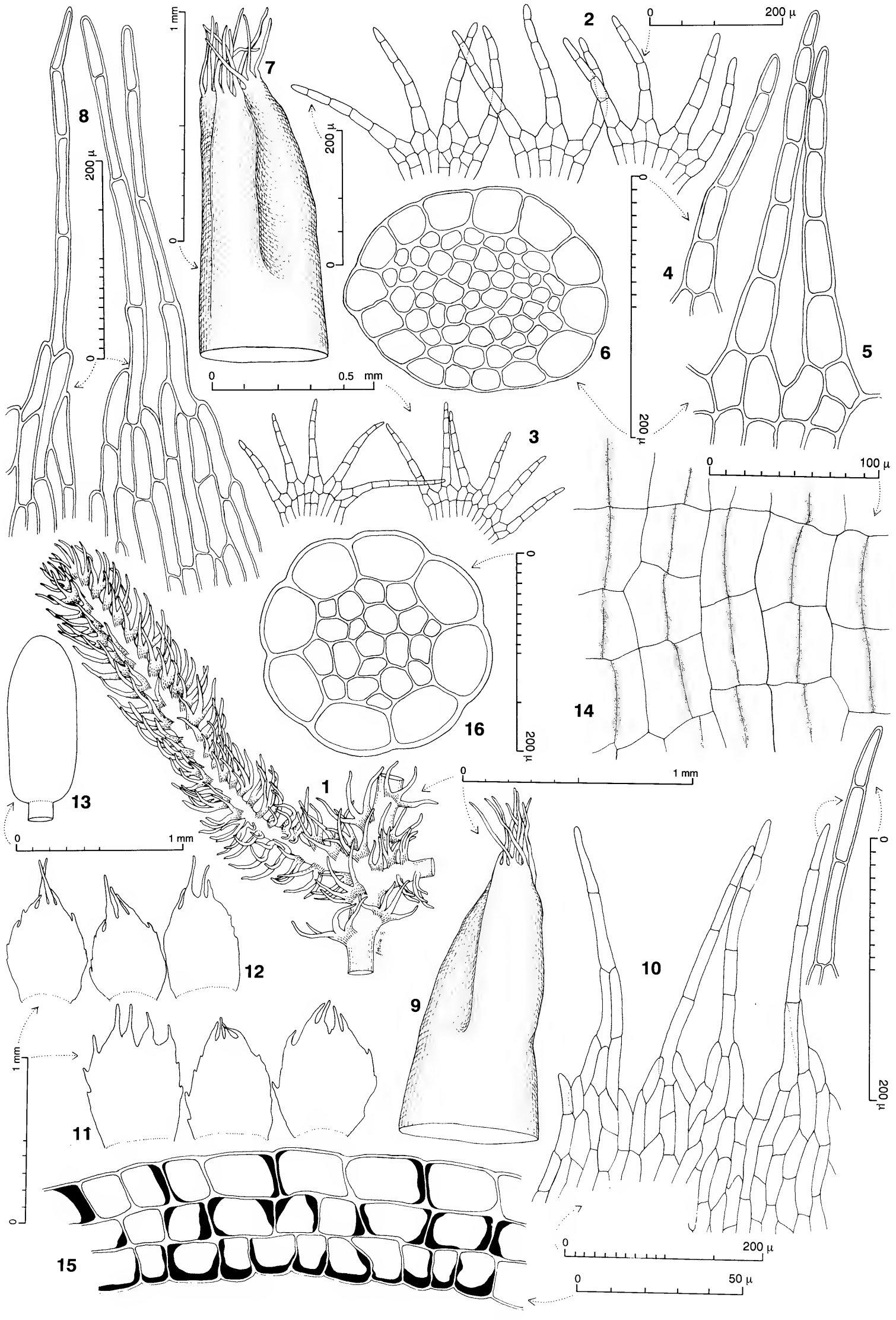

Fig. 68.
Telaranea lindenbergii (Gottsche) J.J.Engel & Merrill (1–8, 11, 13–16) and *Telaranea tetradactyla* (Hook.f. & Taylor) E.A.Hodgs. (9, 10, 12). 1. Sector of main shoot and primary branch, dorsal

Telaranea lindenbergii is readily distinguishable from other *Telaranea* species by the distant, widely spreading, deeply dissected stem leaves (Fig. 68: 1), with a low disc, for the most part only 2 cells high (Fig. 68: 2, 3). The leaves of the main axis are ± transversely inserted and oriented, although the orientation of the branch leaves is variable. Four varieties of the species are recognized, which can be distinguished as follows.

Key to Varieties

1a. Stems flexuous, often appearing somewhat fleshy for plant size, the branches more closely spaced; branches short, of about equal length, hardly tapering, only exceptionally flagelliform, the secondary branches often frequent; plants pale green 2
  2a. Branch leaves ± transversely inserted and oriented. Common throughout New Zealand . . . . . var. *lindenbergii* (p. 328)
  2b. Branch leaves incubously inserted and oriented 3
    3a. Branches terete; lobe cells papillose . . . . . var. *papillata* (p. 328)
    3b. Branches complanate-foliate; lobe cells smooth. . . . var. *complanata* (p. 327)
1b. Stems slender, straight, rather wiry, the branching ± distant; branches long, flagelliform, the secondary branches typically few; plants brownish yellow to rust-brown. Primarily southern South Is. . . . . var. *mellea* (p. 330)

Telaranea lindenbergii (Gottsche) J.J.Engel & Merrill var. ***complanata*** J.J.Engel & Merrill

Telaranea lindenbergii var. *complanata* J.J.Engel & Merrill, Phytologia 79: 252. June 1996 (1995).

Holotype: New Zealand, South Is., Otago Prov., Whare Flat, W of Dunedin, 70 m, *Engel 17641 – c. sporo.* (F).

Branches distinctly complanate-foliate, the branch leaves imbricate, obliquely spreading, incubously inserted and oriented; leaves of main axis variable in insertion, mostly subtransverse to moderately incubous, sporadically strongly oblique to almost longitudinal.

Distribution and Ecology: Endemic to New Zealand: Known from scattered sites on Stewart Island (5–200 m), South Island (120–150 m), North Island (180–570 m). Known from Otago (Dunedin), Volcanic Plateau (Rotorua) and Auckland (Herangi Ra., Kaimai Ra.) EPs.

The variety occurs in humid niches within forests of various types at lower elevations, and may be on rotten logs and on rich humus or clayey soil of banks. It also is present on caudices

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view. 2. Three leaves. 3. Two leaves. 4, 5. Leaf lobes. 6. Stem, cross section. 7. Distal sector of perianth. 8. Portion of perianth mouth. 9. Distal half of perianth. 10. Portion of perianth mouth, the uniseriate row at right shown at higher magnification. 11. ♀ Bracts and, in middle, bracteole. 12. ♀ Bracts and bracteole. 13. Capsule profile. 14. Capsule wall, outer layer, showing two-phase development. 15. Capsule wall, cross section. 16. Seta, cross section. (Figs. 1, 2, 4, 7–8, 11, from *Engel 19300*, New Zealand, South Is., Paparoa Ra., along Croesus Track; 3, 5, from *Allison H79*, New Zealand, North Is., Volcanic Plateau EP, Puaiti Bush; 6, from *Allison 3236*, same loc. as *Allison H79*; 9, 10, 12, from *Child H2353*, New Zealand, South Is., Otago EP, Ross Creek; 13–15, from *Reif C86E*, New Zealand, South Is., Westland EP, Camp Creek; 16, from type of var. *complanata*.)

of *Cyathea dealbata* and *Dicksonia squarrosa* and in such niches may form large colonies; in particularly humid niches it is also found on old, very rotted, prostrate tree-fern trunks.

The Lee Bay site on Stewart Island is of interest. Plants occurred over soil of a drainage area just above the shoreline at the edge of very exposed, coastal scrub that includes *Brachyglottis rotundifolia*, *Carpodetus serratus* and *Coprosma robusta*; the coastal scrub is at the margin of a podocarp–hardwood forest. The niche likely would be exposed to periodic salt spray (see Engel and Schuster, 1973).

Comments: Similar in aspect and branching to var. *lindenbergii*, but differing chiefly in the flattened, comb-like branches with obliquely spreading, incubously oriented leaves. This plant is likely to be confused with *Telaranea tetradactyla*, which also has strongly complanate-foliate branches, but differs in the higher disc of the leaves of the main axis, which is typically 3 or often 4 cells high, vs. 2 or only rarely 3 cells high in var. *complanata*. In addition, the stems of var. *complanata* are stouter, with more numerous, thicker-walled medullary cells. *Telaranea tetradactyla* is also a much softer, laxer plant, with more irregular branching, and is essentially an extreme southern South Island plant.

Telaranea lindenbergii var. ***papillata*** J.J.Engel & Merrill

[Fig. 69]

Telaranea lindenbergii var. *papillata* J.J.Engel & Merrill, Fieldiana, Bot. 44: 83. *f. 26A*. 2004. Holotype: New Zealand, North Is., South Auckland Prov., Whareorino Forest, track to Leitch's Hut, 280 m, *Engel 23773 – c. sporo.* (F); isotype: (AK).

Distribution and Ecology: The type and only known plant occurred on clay banks under a *Blechnum novae-zelandiae* overhang, with *Weinmannia* and *Dicksonia squarrosa* as the dominant forest canopy and with occasional *Leptospermum scoparium*.

Comments: Plants are similar to var. *complanata* in the incubous insertion of the branch leaves, but differ in the terete, not complanate-foliate branches and the roughened surface of the leaf lobes (Fig. 69: 6). The lobes are rather short, 4–5 cells long (Fig. 69: 1–5) vs. 5–6(7) cells long in var. *lindenbergii* (Fig. 68: 2–5).

Telaranea lindenbergii (Gottsche) J.J.Engel & Merrill var. ***lindenbergii***

Lepidozia subverticillata Colenso, Trans. & Proc. New Zealand Inst. 18: 245. 1886. Lectotype (*fide* Engel and Merrill, 2004): New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1420* (WELT! – *c. per.* + *sporo.* + ♂); isolectotype: (BM! – *c.* ♂).

Lepidozia leucocarpa Colenso, Trans. & Proc. New Zealand Inst. 21: 65. 1888 (1889). Lectotype (*fide* Engel and Merrill, 2004): New Zealand, Waipawa Co., near Norsewood, "Shingle splitter's swamp," 1885, *Colenso a. 1320* (WELT! – *c. per.* + *sporo.*); isolectotype: (BM! – *c. per.* + *sporo.*).

Lepidozia minutissima Colenso, Trans. & Proc. New Zealand Inst. 21: 66. 1888 (1889). Type: New Zealand, Waipawa Co., near Dannevirke, 1888, *Colenso a. 1319* (BM!, WELT – *absens*).

Lepidozia occulta Colenso, Trans. & Proc. New Zealand Inst. 22: 456. 1889 (1890). Type: New Zealand, Waipawa Co., S of Dannevirke, 1889, *Colenso a. 1517* (BM! – *c.* ♂, WELT – *absens*).

Lepidozia hepaticola Steph., Sp. Hepat. 3: 592. 1909. Type: New Zealand, without specific loc., *Goebel s.n.* (G!).

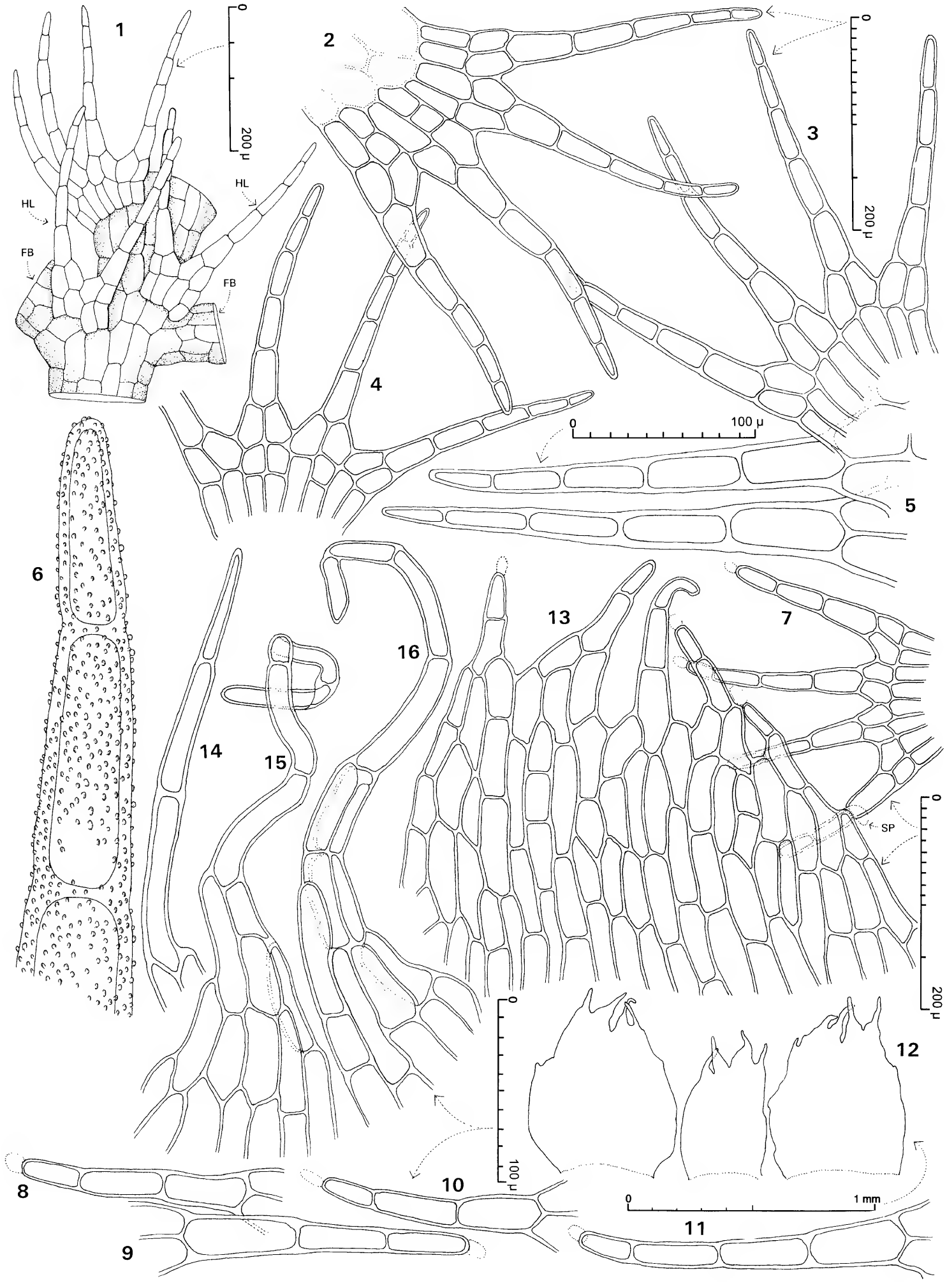

Fig. 69.
Telaranea lindenbergii var. *papillata* J.J.Engel & Merrill. 1. Portion of shoot showing a leaf and 2 half-leaves (= HL) each at the base of a *Frullania*-type branch (= FB), dorsal aspect. 2–4. Leaves (surface detail not shown); all drawn to same scale. 5. Two leaf lobes, surface detail not shown. 6. Distal portion of leaf lobes showing surface papillae (× 1055). 7. Underleaf. 8–11. Underleaf lobes. 12. Innermost ♀ bracts and, in middle, bracteole. 13. Distal portion of ♀ bract (SP = slime papilla). 14–16. Lobes of perianth mouth, all drawn to same scale. (All from type.)

Lepidozia radiata Steph., Sp. Hepat. 6: 339. 1922. *Telaranea radiata* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: New Zealand, sin. loc., "inter Colenso 1095" (G!, WELT! – *c.* ♂).

Plants pale green; stems flexuous, often appearing fleshy for plant size; branches rather closely spaced, of about equal length, hardly tapering, often at right angles to main axis, with secondary branches often frequent; branches terete, not complanate, with leaves typically transversely inserted and oriented (at times weakly incubous), plane or somewhat hand-like due to incurving of lobes; leaf disc 2–3(4) cells high; leaf lobes typically uniseriate to the base, the cells of uniseriate row weakly constricted at septa or sometimes with feebly protruding septa.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands, Stewart Island (530 m), South Island (0–915 m), North Island (30–920 m), Kermadec Islands. For comments on Tasmanian reports see Engel and Merrill (2004). Known from all ecological provinces in South and North islands.

The plant is common throughout New Zealand in low- to middle-elevation forests (typically below 700 m and commonly at sea level). It occurs on a variety of substrates, but commonly may be found on rotted, especially decorticated wood (rather frequently on crumbly wood on the forest floor), bryophyte-covered logs, tree-fern bases (e.g., *Cyathea*), shaded, clayey, mossy banks, damp leaf litter, or less commonly corticolous (e.g., bark of *Kunzea*). It often forms yellow-green, felt-like, at times dense mats. It has been found with *Chiloscyphus mittenianus*, *C. spiniferus*, *Plagiochila gigantea*, *Rhaphidorrhynchium amoenum* and *Schistochila kirkiana.*

Comments: *Telaranea lindenbergii* var. *lindenbergii* has a distinctive aspect, due to the ± regular 1–2-pinnate branching and the rather short primary branches of roughly equal length. The leaf insertion is typically transverse and the disc is only 2 (locally 3) cells high, consisting of a basal tier of narrowly elongate cells, and a distal tier, formed by the bases of the lobes. The lobe cells are commonly moderately thick-walled, and the lobes are either straight-sided or have weakly protruding septa (Fig. 68: 4, 5) and a firm, subcapillary appearance, suggestive of *T. praenitens*. The var. *lindenbergii* is noteworthy for the high incidence of fruiting, with perianths (and often sporophytes) present in a large number of the specimens examined, and androecia also commonly present.

Plants of *Telaranea lindenbergii* often bear a striking resemblance to *T. pallescens*. Both species are very pale to whitish green in color, with transversely inserted, deeply dissected, hand-like leaves. The branches are often subopposite, at right angles to the main shoot, with an abundance of secondary branches. The presence of a hyaloderm and absence of *Microlepidozia*-type branching will immediately mark *T. lindenbergii*. In addition, the disc cells of *T. pallescens* are quite small, short-rectangular to quadrate, and the disc is 2–4(5) cells high.

Telaranea lindenbergii var. ***mellea*** J.J.Engel & Merrill

Telaranea lindenbergii var. *mellea* J.J.Engel & Merrill, Phytologia 79: 252. June 1996 (1995). Holotype: New Zealand, South Is., Otago Prov., near Herbert, *Allison H5674* (CHR); isotype: (F).

Plants brownish yellow to rust-brown; stems slender, straight, rather wiry; branches rather distant, often long-flagelliform, the secondary branches typically few; branches terete, not complanate, the leaves transversely oriented, somewhat hand-like (at least on branches) due to incurving of lobes; leaf disc 2–3(4) cells high; lobes not infrequently with a biseriate tier of

cells between the uniseriate row and extreme base, the cells of the uniseriate row ± thick-walled, weakly constricted or sometimes with feebly protruding septa.

Distribution and Ecology: Endemic to New Zealand: Stewart Island, South Island (150–610 m), North Island. Known from Otago (Dunedin), Western Nelson (Stony Creek near Westport) and Volcanic Plateau EPs.

Known only from a limited number of collections, primarily from the southern portion of South Island. Known also from a single station in North Island, near Rotorua.

Comments: When viewed by transmitted light under the compound microscope, plants of var. *mellea* are often suffused with a brownish yellow to rust-brown pigment, rather like that of honey. The plant also has a distinctive aspect, differing from the typical variety by its straight, wiry stems and distant, long-flagelliform branches.

Telaranea pallescens (Grolle) J.J.Engel & Merrill

Kurzia pallescens Grolle, Rev. Bryol. Lichénol. 32: 177. 1963 (1964). *Microlepidozia quadriseta* fo. *pallescens* (Grolle) R.M.Schust., Nova Hedwigia 15: 456. 1968. *Telaranea pallescens* (Grolle) J.J.Engel & Merrill, Fieldiana, Bot. 44: 87. 2004. Holotype: New Zealand, North Is., NW Ruahines, Otupae Station, 1948, *Druce* (MPN ex hb. Hodgson 8223, *non vidi*).

Kurzia quadriseta Grolle, Rev. Bryol. Lichénol. 32: 175. *pl. 2*. 1963 (1964), *non Lepidozia quadriseta* Steph., Sp. Hepat. 3: 582. 1909 (≡ *Telaranea quadriseta* (Steph.) J.J.Engel & Merrill). *Microlepidozia quadriseta* (Grolle) R.M.Schust., Nova Hedwigia 15: 456. 1968. Holotype: Tasmania, Williamsford, near Mt. Read, 1 Jan. 1900, *Weymouth 5755* as *Lepidozia longiscypha* (M, *non vidi*); isotype: (G!).

Plants with the aspect of *Telaranea lindenbergii*, prostrate and densely interwoven, rarely subcaespitose, pale whitish green or at times pure green, nitid when dry; shoots to 6 mm wide including branches. Branching irregularly 1-pinnate to ± regularly 1–2(3)-pinnate, the branches dorsally ascending to suberect, typically with *Frullania*-type branches on one side of the main axis and *Microlepidozia*-type on the other; branch half-leaf of *Frullania*-type branches (1)2–3-lobed nearly to the base, the first branch underleaf 2–3-lobed, inserted on the lateral side of branch base or the juncture of main shoot and branch, aligned with underleaves of branch. Ventral-intercalary branches occasional; lateral-intercalary branches not seen. Stem cortical cells moderately thick-walled, in 12–16 rows, the medullary cells 15–20, somewhat smaller. Leaves stiffly and widely spreading, transversely inserted, symmetrically (3)4–6-lobed, 280–700 μm wide (between tips of lobes) × 260–350 μm long; branch leaves 4-lobed, subcontiguous, feebly succubously oriented. Lobes uniseriate to base, inserted on a triangular base composed of 2–3(4) disc cells, the uniseriate portion 5–6(7) cells long, the cells firm and rather thick-walled, gradually smaller distally, the cells 2–4.7:1, gradually shorter distally; surface smooth. Disc 10–12 cells broad at base, 2–4(5) cells high (including base of lobes). Cells of disc differentiated in size and shape from those of the lobes, compact, short-rectangular to subquadrate, 16–24 μm wide × (16)24–28(40) μm long; surface smooth. Oil-bodies (Schuster, 1980a, fig. 2: 2) (1)2–3 in cells of disc, 3–5 per cell in uniseriate row of lobe, weakly to distinctly botryoidal. Underleaves 4–6-lobed, often with 1 or more lobes abbreviated, terminating in a slime papilla, the disc 2–3 cells high.

Dioecious. Androecia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from main shoot or terminal on rather short to long primary or (more often) second-

ary terminal branches; bracts concave, the disc especially so, 2–3-lobed to ca. 0.5, the lobes 2 or more cells wide at base, apiculate to short-acuminate, terminating in a uniseriate row of several cells; dorsal margin of disc slightly dilated, with a few crenulations and slime papillae; antheridia 1 per bract, the stalk uniseriate. Gynoecia on abbreviated ventral-intercalary branches from main axis; bracts of innermost series much larger than leaves, the bracts concave, narrowly ovate; apices with 2–4 narrow lobes that terminate in a single cell or a uniseriate row of 2–3 cells, the lobes composed of ± regularly rectangular cells, the apical end of the marginal cells sometimes feebly diverging, the margins at times with a partially or wholly laterally free cell, the lobe margins thus finely and sparingly crenulate-spinose dentate; lamina composed of ± regularly short-rectangular cells, the margin bordered by cells of variable shape, most long and narrow, a few only slightly longer than wide, the apical or free end of marginal cells at times divergent and forming a short projection or an apically oriented tooth, the margin irregularly and sparingly crenate-denticulate, the teeth rarely composed of more than 1 cell; bracteole similar in size and form. Perianth large, fusiform, hyaline, ± terete below, bluntly trigonous only in the distal portion, the mouth strongly contracted and pluriplicate, dentate-ciliate, the teeth free for varying lengths (at times ca. 0.5 of cell free), at times consisting of a uniseriate row of 2 cells; perianth unistratose to base.

Seta with 8 rows of large epidermal cells surrounding an inner core of numerous smaller cells. Capsule ellipsoidal-cylindrical, 490–515 μm wide, 985–1200 μm long, the wall largely 3-stratose, 32–36 μm thick (locally 4-stratose and 35–38 μm thick); outer layer with somewhat irregular two-phase development, the primary cells with walls remaining colorless, the secondary walls with strong, brown, sinuous-nodular thickenings; innermost layer with cells ± irregular in shape, with semiannular bands remote, well-developed and almost always complete.

Spores 12–14 μm in diam., the wall rather thin, honey-colored, with close vermiculate to granular-vermiculate ridges, which are often furcate but do not delimit areolae. Elaters feebly twisted, 7.2–9.5 μm wide, bispiral, the spirals 2.8–3 μm wide.

Distribution and Ecology: New Zealand: South Island (75–1970 m), North Island (10–800 m); Australia: Tasmania. In New Zealand known from Fiordland, Westland, Western Nelson, Canterbury (Main Divide at Arthur's Pass), Sounds–Nelson (Richmond Ra.), Taranaki (Pukeiti Bush), Auckland (Kaimai Ra., Coromandel Forest Park, Waitakere Ra.) and Northland EPs.

In New Zealand it occurs sporadically, over a broad ecological amplitude (often in humid sites), from the southern part of South Island to the northern extremity of North Island. It occurs in forests of several different types on both South and North islands. For example, in the South Island the species grows in seepage areas (with *Telaranea remotifolia*) among cliffs and boulders in a *Nothofagus menziesii* forest (Haast Pass area); on the floor of open boggy areas in a rather open *Leptospermum* scrub forest in a serpentine area (Red Hills, Marlborough); as well as in humid niches with the moss, *Distichophyllum kraussei*, in forest dominated by *Phyllocladus alpinus*, *Nothofagus solandri*, *Leptospermum scoparium*, *Olearia lacunosa* and *Weinmannia racemosa* (Paparoa Ra.). It is present in several different types of lowland bogs and is found, for example, in *Sphagnum – Empodisma minus – Halocarpus* bogs with *Kurzia helophila*, *Megalembidium insulanum* and *Riccardia* sp. (Omoeroa River, *Schuster 67-246*), in pakihi along the west coast of South Island, as well as on wet soil among sedges and *Gleichenia* at an ecotone between *Typha orientalis* swamp and *Leptospermum scoparium* swamp (south of Cape Reinga, Northland). In the North Island it grows, for example, over soil on stream banks just above water level in old *Kunzea* forest with *Agathis australis* and *Phyllo-*

cladus trichomanoides (Waitakere Ra., Auckland) and on well-shaded, bryophyte-covered stream banks, again not far above water level, in kauri forest with *Weinmannia silvicola* (Waipoua Forest). At Aongatete River (Kaimai Ra., 425 m) it was on soil over bedrock, deep in a pocket-like drainage channel at the river margin where it may occasionally be inundated. The river is at the bottom of a narrow ravine with a dense overhang of *Blechnum* and *Freycinetia baueriana* in *Dacrydium cupressinum – Beilschmiedia tawa* forest with a *Cyathea* understory. On Mt. Moehau (Coromandel Forest Park, ca. 800 m) plants grew intermingled in *Sphagnum* on the bank of a very moist seepage area in a mosaic of *Sphagnum* bog and small communities of shrub-heath including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus*, *Corokia buddleoides*, with occasional stunted *Weinmannia silvicola* and stunted *Dacrydium cupressinum*. It has been found with *Balantiopsis diplophylla*, *Cryptochila grandiflora*, *Heteroscyphus billardierei*, *Isotachis montana*, *Kurzia helophila*, *Lepidozia spinosissima*, *Riccardia cochleata*, *R. pennata*, *Sphagnum cristatum* and *Treubia pygmaea*.

The species extends into the penalpine and alpine zones and is present in a variety of humid sites, including the sides of rills and watercourses, soil on tussock bases and protected shaded niches under shrub cover. In the Arthur's Pass area it is found in a mosaic of penalpine scrub and alpine vegetation at the sides of tussock plants that grow at the edges of pools and, interestingly, *Telaranea pallescens* may form large masses semi-submerged in the pools. In the alpine zone in Gertrude Valley (Fiordland) it occurs on protected ledges in seepage areas of cliffs.

Comments: *Telaranea pallescens* is a rather uncommon plant and is most likely to be mistaken for *T. lindenbergii*, a common species in New Zealand. The two species are remarkably similar in appearance, due to their ± wiry, bristly appearance, regularly pinnate branching and pale whitish green color. The leaves are transversely inserted and deeply 4–6-lobed, the lobes uniseriate to the base and inserted on 2 disc cells, with a disc 2–4 cells high. Differences include the presence of *Microlepidozia*-type branches and asymmetrically lobed underleaves in *T. pallescens*. The most conspicuous difference, however, may be in the basal tier of cells of the leaf disc, which in *T. lindenbergii* are thin-walled and longitudinally elongated (17–24 μm wide × 40–60 μm long, Fig. 68: 2, 3) vs. small, compact and subquadrate in *T. pallescens* (ca. 24–28 μm wide and long, Schuster, 1980a, fig. 2: 9–11). *Telaranea trilobata* differs from *T. pallescens* in the mostly 3-lobed leaves and less strongly differentiated cells of the leaf disc.

Telaranea trilobata (R.M.Schust.) J.J.Engel & Merrill

Kurzia quadriseta var. *trilobata* R.M.Schust., J. Hattori. Bot. Lab. 48: 363. *f. 3*. 1980. *Telaranea trilobata* (R.M.Schust.) J.J.Engel & Merrill, Fieldiana, Bot. 44: 89. 2004. Holotype: New Zealand, North Is., Tongariro Natl. Park, Soda Springs, head of Mangatepopo Stream, near saddle between Mts. Ngauruhoe and Tongariro, ca. 4500 ft., *Schuster 5110a* (F).

Plants light green to grass-green, with whitish stems, in densely interwoven mats or caespitose and erect, nitid when dry; shoots to 5 mm wide (including branches). Branching irregularly and rather sparingly 1-pinnate, with branches of the *Frullania* type on one side, *Microlepidozia* type on the other, the branches suberect to ascending; branch half-leaf of *Frullania*-type branch undivided to 2-lobed nearly to base, the first branch underleaf undivided to 2–3-lobed, inserted on the ventral-lateral side of branch base or the juncture of main shoot and branch and aligned with underleaves of branch; first appendage (ventral half-leaf) of *Microlepidozia*-type branch bilobed or undivided. Ventral-intercalary branches occasional, leafy or

geotropic and stoloniform; lateral-intercalary branches occasional to rather freely produced. Stem with cortical cells moderately thick-walled, in 9–12 rows, larger than the medullary cells, which are in 6–7 to 12–14 rows. Leaves strongly spreading, approximate, transversely inserted, symmetrically 3(4)-lobed, 350–475 μm wide (500–550 μm wide in 4-lobed leaves) × 350–450 μm long, the lobes divergent; branch leaves subcontiguous, weakly succubously oriented, mostly 3-lobed. Lobes ciliiform, uniseriate to the base, inserted on a triangular base composed of 2–4 cells, sporadically with an additional biseriate tier above the base, the uniseriate portion 4–5 cells long, the lobe cells elongated (2–3:1), gradually shorter distally, rather thick-walled; surface smooth or finely striate-papillose. Disc 6–8 cells broad at insertion, 2(3) cells high, including basal cells of lobes. Cells of disc not much differentiated from lobe cells, oblong to rectangular, 22–30 μm wide × 48–64(72) μm long; surface smooth or finely striate-papillose. Underleaves 3(4)-lobed, the lobes mostly 4 cells long, uniseriate or 2-seriate in basal tier, formed of elongated cells as on leaves, the middle lobe often abbreviated, terminating in a slime papilla; disc 6–8 cells wide, 1–2 cells high, the cells small and ± isodiametric.

Dioecious. Androecia not seen. Gynoecia (only juvenile known) on short lateral-intercalary branches.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5 m), South Island (430–680 m), North Island (1230–1370 m). Known from Fiordland (Borland Burn), Westland (Haast Pass) and Volcanic Plateau (Mt. Ruapehu) EPs.

Known from only a few collections, all in humid micro-niches. On Stewart Island the species was found near sea level in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. At this site the species occurred on the floor under very dense *Gleichenia* cover adjacent to a water channel. In the southern sector of the South Island the species occurred at 680 m on a protected rock face at the margin of a waterfall within a *Nothofagus* forest (Fiordland Natl. Park, above South Branch of Borland Burn). At the Blue River–Makarora River confluence (Aspiring Natl. Park, 430–480 m) the species occurred on vertical, dripping, cliff faces under *Blechnum* cover in a bryophyte-rich *Nothofagus menziesii* forest. It occurred on Mt. Ruapehu (Blyth Track, ca. 0.5 km from Ohakune Mtn. Road, Tongariro Natl. Park, ca. 1230 m) over soil on the lip of a stream bank within a forest dominated by *Nothofagus solandri* var. *cliffortioides*. The type was growing on moist volcanic soil in rocky areas along a stream, in a penalpine open area, associated with *Temnoma quadrifidum* and *Triandrophyllum subtrifidum* at 1370 m.

Comments: *Telaranea trilobata* most closely resembles *T. pallescens*, differing chiefly in the predominantly 3-lobed leaves and less sharply differentiated disc cells. The plants are regularly and suboppositely branched, with *Microlepidozia*-type branches on one side of the shoot and *Frullania*-type branches on the other. The underleaves in *T. trilobata* are dissimilarly 3–4-lobed, with 1–2 lobes abbreviated and ending in a slime papilla, and, like the leaves, have a distinct basal tier of cells at the base of the disc. The cortical cells of the stem are in 9–12 rows, with 6–7 to 12–14 rows of medullary cells.

Telaranea fragilifolia (R.M.Schust.) J.J.Engel & Merrill

Kurzia fragilifolia R.M.Schust., J. Hattori Bot. Lab. 48: 364. *f. 4*. 1980. *Telaranea fragilifolia* (R.M.Schust.) J.J.Engel & Merrill, Fieldiana, Bot. 44: 90. 2004. Holotype: New Zealand, Little

Barrier Is., summit track to Mt. Hauturu, SE of summit of Mt. Herekohu, 1700–1900 ft., *Schuster 57896* (F).

Plants delicate, loosely creeping to suberect, pale green, nitid; shoots to 560 μm wide, with leaves. Branching irregularly and remotely branched, with *Frullania*- and *Microlepidozia*-type branches and lateral-intercalary branches produced; lateral-intercalary branches at times present nearly to the exclusion of other branch types; ventral-intercalary stolons or flagella rarely present; half-leaf of *Frullania*-type branch undivided or bilobed, the first branch underleaf undivided, inserted on ventral side of branch at base; ventral half-leaf of *Microlepidozia*-type branch undivided. Stems slender and delicate, the cortical cells in 8–9 rows, faintly striolate, thin-walled, much larger than the medullary cells, which are in 6–13 rows. Main shoots and branches with 2–3 cortical cells intervening between successive leaves on either side, the leaves on prolonged, slender axes more distant, to 9 cells apart. Leaves remote, rather widely spreading, the insertion transverse, ca. 300–340 μm long, asymmetrically to ± symmetrically 3-lobed almost to the base, the lobe bases (basal tier) biseriate, connate for ca. 0.5 or somewhat less, or the basal cells completely united, with the tier above partly united, forming a disc 1.5 cells high, occasionally with an additional biseriate tier at base of lobes; branch leaves bifid. Lobe tips caducous, at times only the basal cells of the lobes remaining, the lobes subequal to unequal, the dorsal-most lobe then somewhat shorter; lobes gradually tapering from base to apex, ± straight, biseriate at the base (at times with an additional biseriate tier), the intact lobes with a uniseriate row of 4–6 cells; cells of basal tier 24–31 μm wide × 48–60 up to 86–95 μm long, the basal cell of uniseriate row 28–34 × 72–84 μm, the next cell shorter and narrower; terminal cell (in intact lobes) not distinctly shorter than the penultimate cell; lobe cells rather firm-walled, the transverse septa not projecting, the lobe straight-sided or at times weakly constricted at the septa; surface faintly to distinctly striolate. Underleaves trifid, with 1–2 lobes abbreviated, consisting of a uniseriate row of 3–4 cells arising from a geminate base, terminating in a slime papilla.

Dioecious. Androecia not seen. Gynoecial branches (type) very short, all ventral-intercalary in origin.

Distribution and Ecology: New Zealand: South Island (45 m), North Island (5–580 m); Australia: Tasmania. In New Zealand known from Westland (Jackson River) and Auckland (Kopuatai Peat Dome, Little Barrier Island) EPs.

The species is known only from three stations in New Zealand. The type (Little Barrier Island) reportedly occurred with material of *Lembidium longifolium* on shaded, permanently moist rock walls, in transition from *Agathis australis* forest to *Beilschmiedia tawa – Weinmannia* forest. Plants from the Cascade Road (South Westland, 45 m) occurred over soil in a protected pocket on a large vertical roadside bank at the margin of mature *Nothofagus menziesii* forest. The banks are bryophyte covered (dominated by *Isotachis* sp.) with *Fuchsia excorticata* at the base of the bank. The plant from Kopuatai Peak Bog (Hauraki Plains, Waikato) occurred in ground cover with *Goebelobryum unguiculatum* and *Riccardia crassa* under a *Sporadanthus ferrugineus*–dominated canopy with *Empodisma minus* and *Leptospermum scoparium* present (see de Lange et al., 1999). The Tasmanian collection occurred with *Telaranea herzogii* in *Eucalyptus obliqua* wet-sclerophyll forest at 130 m.

Comments: This species is notable for its highly fragile, caducous leaf lobes and presence of lateral-intercalary branches, which in several populations are abundantly produced, to the almost complete exclusion of other branch types.

Telaranea tetradactyla (Hook.f. & Taylor) E.A.Hodgs.
[Fig. 68: 9, 10, 12; Fig. 70]

Jungermannia tetradactyla Hook.f. & Taylor, London J. Bot. 3: 286. 1844 (3: 286 [*sic*] *in errore pro* 386). *Lepidozia tetradactyla* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 213. 1845. *Mastigophora tetradactyla* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Neolepidozia tetradactyla* (Hook.f. & Taylor) Fulford & J.Taylor, Brittonia 11: 84. 1959. *Telaranea tetradactyla* (Hook.f. & Taylor) E.A.Hodgs., Rec. Domin. Mus. 4: 106. 1962. Lectotype: Auckland Is., Nov. 1840, on *Jungermannia coalita*, *Hooker* (FH!); isolectotypes: (BM! [2 seen]).

Telaranea longii Paton, J. Bryol. 17: 289. *f. 1.* 1992. Holotype: Scotland, Argyll, near Dunoon, foot of Glen Massan, Younger Botanic Garden, 40 m, *Long 14231* (E!); isotypes: (E!, herb. Paton; NY!).

Plants delicate, flexuous yet firm, procumbent, in compact, soft, silky, felt-like mats, normally silvery- to pure green; plants small, to ca. 5 mm wide, including branches. Branching somewhat irregularly 1(2)-pinnate, the branches of the *Frullania* type, complanate, the branch leaves incubously inserted and shingled; branch half-leaf bifid, the lobes diverging; first branch underleaf undivided and ciliiform, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, leafy, sometimes becoming leading shoots. Stems with cortical cells distinctly differentiated, thin-walled, in 12–13 rows; cortical cells in section much larger than the numerous (ca. 18–36) medullary cells. Rhizoids often copiously produced from cells of underleaf disc. Leaves on main shoot obliquely spreading, contiguous to loosely imbricate on main stems and closely imbricate on the branches, plane to moderately convex (due to broad, slight incurving of lobes), the leaves (of main axis) with insertion weakly to distinctly incubous, the branch leaves moderately to distinctly incubously inserted and oriented; leaves 220–320 μm wide (when lobes parallel) to 390–540 μm wide (when lobes divergent) × 490–630 μm long, symmetric to weakly asymmetric, 4(6)-lobed to 0.6–0.75, the lobes longer than disc height. Lobes ciliiform, uniseriate throughout and inserted on a triangular base composed of 2–3 disc cells or, often, with a base of (2)3–4 laterally juxtaposed cells and 1(2) additional biseriate tiers between the base and uniseriate row, the uniseriate portion (5)6(7) cells long, with cells ± thin-walled, often weakly to moderately constricted at the septa; surface smooth. Disc ± symmetrically short-cuneate, (2)3–4 cells high (from median sinus base to leaf base) including paired cells at bases of lobes, 8 cells wide in 4-lobed leaves, 12 cells wide in 6-lobed leaves. Cells of disc thin-walled but firm, ± equal in thickness to those of lobe cells, trigones lacking, the largest cells (in median sector of disc) 28–41 μm wide × 48–64 μm long; basal tier of disc cells often longitudinally elongate; surface smooth. Underleaves much smaller than leaves, strongly spreading, distant, plane to slightly incurved, 4-lobed to ca. 0.8, the lobes ciliiform, the uniseriate portion formed of 3–4 somewhat elongated cells, terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide. Rhizoid initial cells small, subquadrate, formed from some distal cells of underleaf disc.

Plants dioecious. Androecia either terminal or intercalary on short to moderately long primary or secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary, spicate branches; bracts closely imbricate, dorsally assurgent, deeply concave-subcucullate, 2-lobed to ca. 0.5–0.6, the lobes acuminate to subcaudate, terminating in a uniseriate row of 4–5 somewhat elongated, thin-walled cells, the terminal cell rounded at the summit; dorsal margin of lamina somewhat dilated and incurved, crenulate and with a few slime papillae or with a 1- to several-celled, sharp tooth; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent. Gynoecia with bracts small for perianth size, those of innermost series concave, short-ovoid, shallowly (3)4-lobed, the 2 median lobes normally larger, the median

lobes subcaudate, terminating in a uniseriate cilium of 3–4 elongated cells, with a terminal slime papilla, the lateral processes shorter, the ciliiform process consisting of a single cell or a uniseriate row of 2 cells; lamina composed of ± regularly subrectangular cells, the margins curved, with a few crenations and blunt teeth each formed by the protruding apical end of a marginal cell that is free for varying lengths, a single cell at times entirely laterally free, rarely with a tooth consisting of a uniseriate row of 2 cells, the margins thus crenate-dentate; bracteoles similar in form and size to bracts. Perianth long-emergent, terete in basal sector, obscurely trigonous and basically 3-plicate above, the perianth narrowing toward the contracted mouth; mouth fringed with 12 caudate lobes, the lobes each with a base composed of 3–5 laterally juxtaposed, moderately elongate cells and often a lateral, single-celled spinose tooth, the lobes each terminating in a cilium composed of a uniseriate row of (2)3–5 elongate, thin-walled cells, the basal 1–2 cells 11–14 μm wide × 42–76 μm long (4.1–6.3:1).

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: Campbell Island (100 m), Auckland Islands, Antipodes Islands, Snares Islands, Solander Island (100 m) and Muttonbird Islands, Chatham Islands (80–240 m), Stewart Island (*fide* Hodgson, 1956, p. 605), South Island (15–1170 m), North Island (930–1160 m); adventive in Britain, as *Telaranea longii*. Rather widely cited outside of our area and was previously understood to be an amphi-Pacific species; for a discussion of extraterritorial records see Engel and Merrill (2004). Known from Fiordland, Southland (Bluff), Otago (Dunedin), Westland (Haast Pass), Canterbury (Rockwood Ra.) and Gisborne (Urewera Natl. Park) EPs.

Telaranea tetradactyla, as delimited by Engel and Merrill (2004), is restricted in New Zealand to the subantarctic and southern offshore islands, the southern sector of the South Island and two stations in the North Island (both in Urewera Natl. Park).

In New Zealand the species occurs in shaded, damp, protected niches in lower- to middle-elevation forests as well as penalpine sites. For example, it occurs on rock, deep in protected niches between boulders in a stream valley with *Chionochloa*, *Hebe* and *Dracophyllum* near Mt. Burns (Fiordland, 1010–1170 m). *Telaranea tetradactyla* is not an "abundant species" as stated by Schuster (2000a, p. 216).

Comments: This name has previously been loosely applied to the common, widespread and weedy plant here recognized as *Telaranea lindenbergii* (p. 324). *Telaranea tetradactyla s. str.* has a more restricted distribution and is best characterized by the lax, incubously shingled stem and branch leaves (Fig. 70: 1), giving the plants a soft, silky aspect. The leaf disc is typically 3 (and often 4) cells high vs. 2 (rarely 3) cells high in *T. lindenbergii*. Plants of this species are rarely encountered with perianths, and in our experience, sporophytes are unknown. This is in sharp contrast to *T. lindenbergii*, which characteristically bears perianths (and often sporophytes), as well as androecia.

Both *Telaranea tetradactyla* and *T. lindenbergii* have the perianth mouth long-ciliate (Fig. 68: 7, 9); however, in *T. tetradactyla* and *T. lindenbergii* var. *complanata*, the cells of the uniseriate cilia are thin-walled and relatively short, at most 90 μm long (Fig. 68: 10), vs. thick-walled and 96–130 μm long in *T. lindenbergii* var. *lindenbergii* (Fig. 68: 8).

"*Telaranea trilobata*" (Schuster, Beih. Nova Hedwigia 118: 220. *f. 70*. 2000, *nom. inval. sin. descr. lat.*) was based on a specimen from New Zealand (Doubtful Sound, *Schuster 52883*). According to Schuster (p. 220), this plant is very close to *T. tetradactyla*. We have not seen the specimen.

For comments on nomenclature see Engel and Merrill (2004).

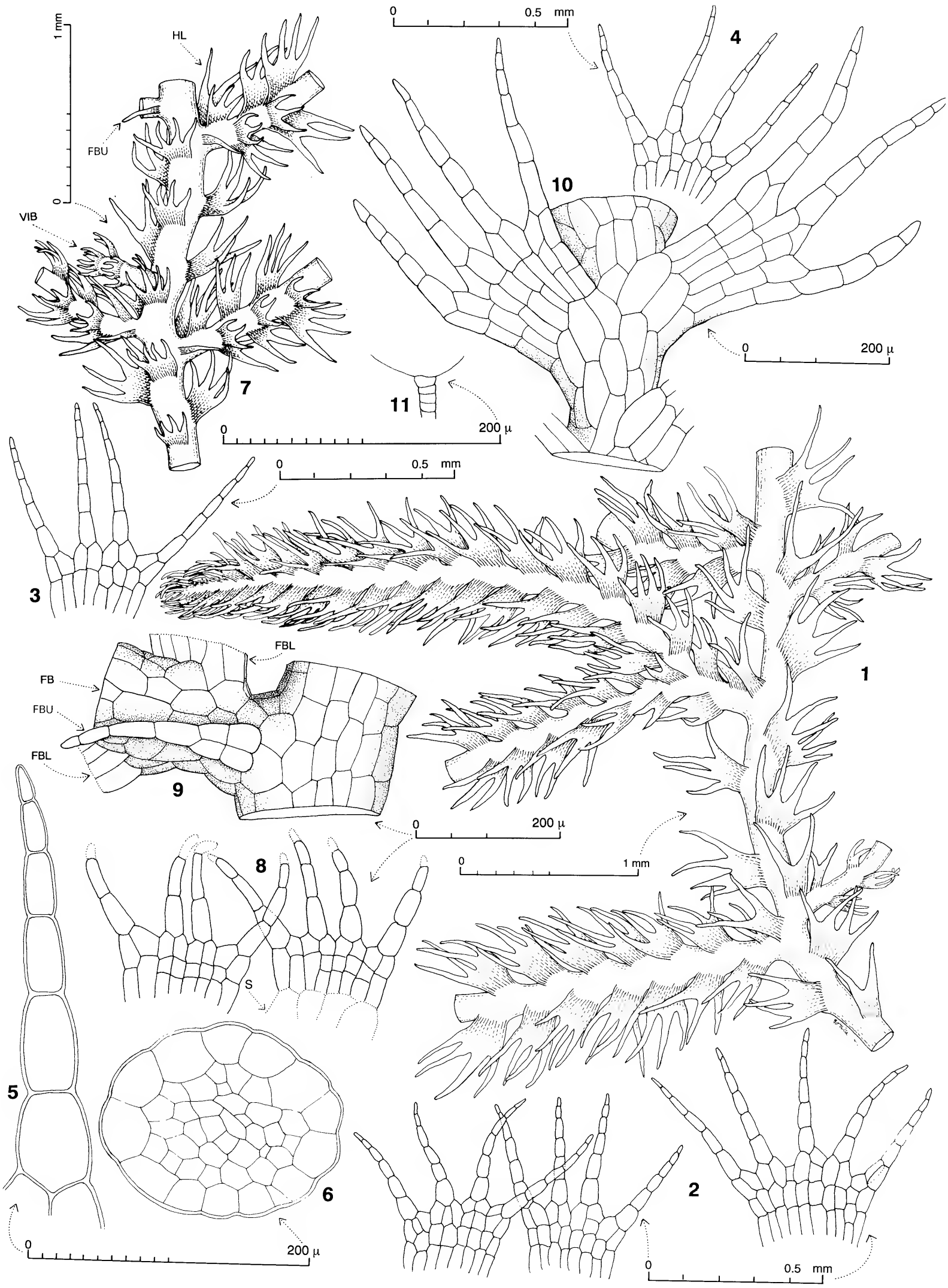

Fig. 70.
Telaranea tetradactyla (Hook.f. & Taylor) E.A.Hodgs. 1. Sector of main shoot with several terminal branches, dorsal view. 2. Four- and 5-lobed leaves. 3, 4. Leaves. 5. Leaf lobe. 6. Stem, cross section. 7. Sector of main shoot (HL = half-leaf; FBU = first branch underleaf; VIB = ventral-

Sect. ***Telaranea***

Kurzia subg. *Nanolepidozia* R.M.Schust., J. Hattori Bot. Lab. 48: 353. 1980. Type: *Lepidozia bisetula* Steph.

Telaranea martinii (E.A.Hodgs.) R.M.Schust.

[Figs. 71, 72; Fig. 77: 3, oil-bodies, p. 355]

Lepidozia martinii E.A.Hodgs., Trans. Roy. Soc. New Zealand 83: 602. *pl. 1, f. 11*. 1956 ("*martini*"). *Telaranea martinii* (E.A.Hodgs.) R.M.Schust., J. Hattori Bot. Lab. 26: 256. 1963. Holotype: New Zealand, North Is., road to Dawson Falls, Mt. Egmont, 2000–3000 ft., Jan. 1955, *Hodgson 10220* (MPN! – *c.* ♂ + *sporo*.).

Plants delicate, flexuous yet firm, loosely procumbent, pale green, nitid; plants small, the main shoots (595)600–840 μm wide. Branching sparingly and irregularly 1-pinnate, the branches of the *Frullania* type; branch half-leaf undivided and subulate to ± narrow-linear, very rarely bilobed; first branch underleaf at base of branch, ± symmetrically or somewhat asymmetrically bilobed, typically consisting of a slender, divergent lobe with a uniseriate row of 3 rather elongate cells, the tip cell lacking a slime papilla, and a shorter, often ± appressed lobe aligned with the branch and consisting of (1)2 rather short cells, the tip cell with a slime papilla. Ventral-intercalary branches occasional, leafy or flagelliform. Stems with cortical cells distinctly differentiated, in 9 rows of cells much larger than those of the medulla; medullary cells consisting of an outer row of 6(7) cells and, within, a core of 3 cells that are smaller than those of the outer ring. Rhizoids sparsely developed, from either tier of underleaf disc cells. Leaves on main shoot widely spreading, contiguous to feebly imbricate both on main stem and branches, plane or nearly so, the insertion distinctly incubous both on main stems and branches; leaves 175–525 μm wide × 330–455 μm long, ± symmetric to weakly asymmetric (the ventral lobe sometimes weaker), 3-lobed to 0.5–0.7 (exceptionally with some 4-lobed leaves, 2-lobed on branches and weaker sectors of main shoot), the lobes longer than disc height. Lobes narrowly attenuate to ciliiform, consisting of a uniseriate row of (2)3–4(5) cells inserted on a triangular base composed of 2–3(4) laterally juxtaposed cells, often with 1(2) additional biseriate tiers between lobe base and uniseriate row in 1 or more lobes (particularly the dorsal and middle lobes), the cells of uniseriate portion thin-walled, not or weakly constricted at the septa and somewhat thickened in the corners; surface of lobe tips finely roughened to indistinctly striate-papillose or smooth. Disc ± symmetrically short-cuneate to subrectangular, 2–4(5) cells high (from dorsal sinus base, including paired cells at bases of lobes), 6–7 (exceptionally 10) cells wide. Cells of disc thin-walled but firm, trigones minute or lacking, the largest cells 24–36(42) μm wide × (30)42–52 μm long; basal tier of disc cells often somewhat longitudinally elongate; surface smooth. Oil-bodies pale, smokey grey, coarsely

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intercalary branch), ventral view. 8. Underleaves; stem cells (= S) stippled in at right. 9. Sector of main shoot, ventral view, showing base of *Frullania*-type branch (= FB) and first branch underleaf (= FBU) (FBL = bases of first branch leaves). 10. Leaf pair of primary branch, dorsal view. 11. Antheridium. (Figs. 1, 2, 5–10, from type of *T. tetradactyla* [FH]; 3, 4, from *Engel 17967*, New Zealand, South Is., Westland EP, summit of Haast Pass, 570 m, *Engel 17967*; 11, from *Child 991*, New Zealand, South Is., Otago EP, Akatore, 38 km SW of Dunedin.)

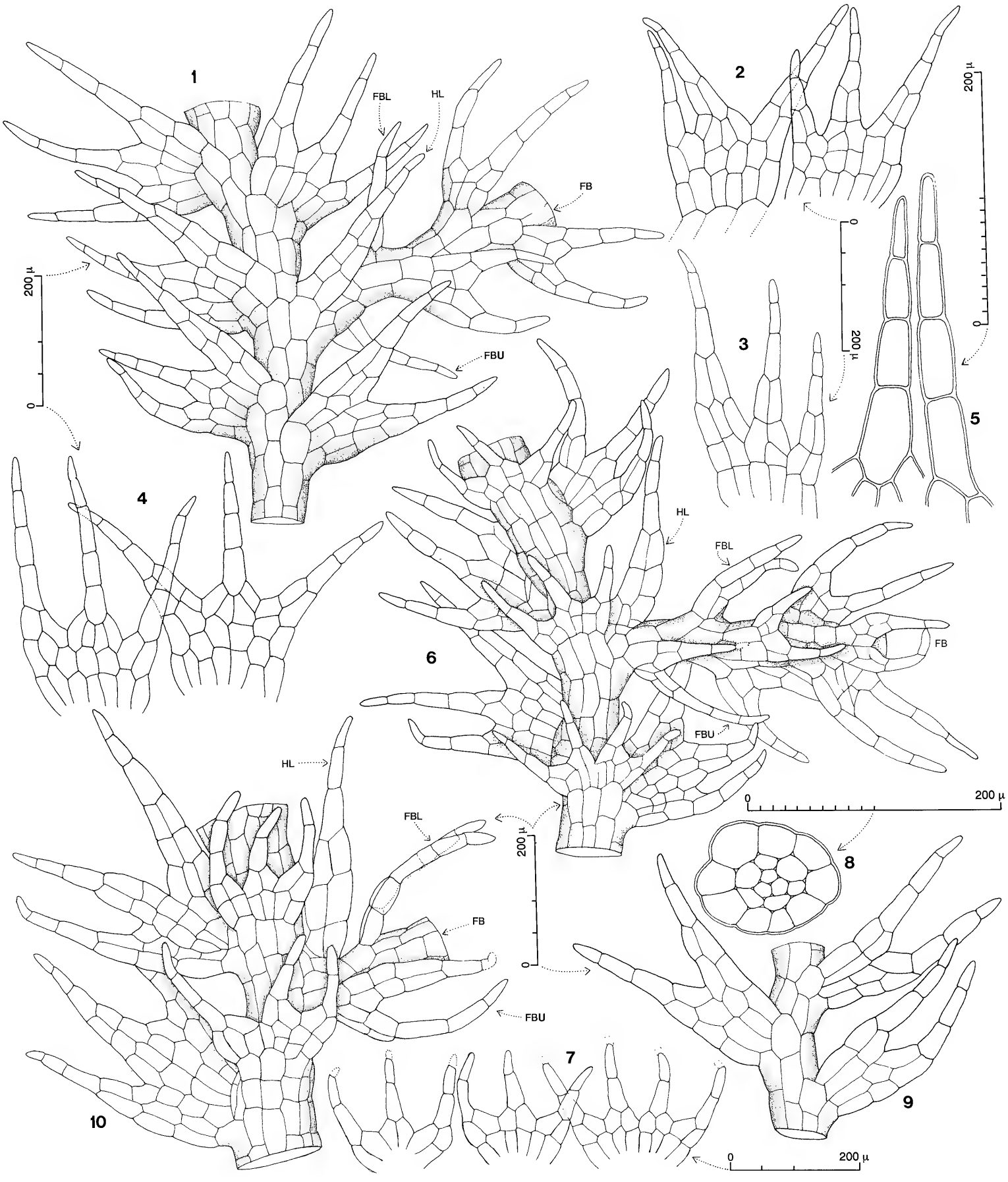

Fig. 71.
Telaranea martinii (E.A.Hodgs.) R.M.Schust. 1. Sector of main shoot showing base of *Frullania*-type branch, dorsal view (= FB) (HL = half-leaf; FBU = first branch underleaf; FBL = first branch leaf, note 1 of the 2 lobes not in view; note also 2-lobed leaf on main shoot at right base). 2–4. Leaves. 5. Leaf lobes. 6. Sector of main shoot of somewhat weaker phase showing base of *Frullania*-type branch, ventral view (= FB) (FBU = first branch underleaf; FBL = first branch leaf; HL = half-leaf). 7. Underleaves. 8. Stem, cross section. 9. Portion of *Frullania*-type branch showing incubous insertion of the bilobed leaves. 10. Sector of main shoot showing base of *Frullania*-type branch, ventral view (= FB) (FBU = first branch underleaf; FBL = first branch leaf; HL = half-leaf). (All from type.)

granular, the spherules only slightly protruding beyond membrane, the median disc cells with ca. 6 oil-bodies per cell, the oil-bodies irregular in shape, narrowly to broadly elliptic to subcrescentic, at times appearing pinched, 6.3–6.8 × 9.7–12.3 μm, a few ca. 7.2 × 16.4 μm. Underleaves much smaller than leaves, widely spreading to squarrose, distant, plane, 3(4)-lobed (bilobed on weaker sectors of main shoot), the lobes ciliiform, the uniseriate portion formed of 2(3) slightly elongated cells, terminating in a slime papilla, the underleaves sometimes weakly asymmetric, with one lobe longer and lacking a slime papilla; disc abbreviated, 2 cells high. Asexual reproduction lacking.

Plants monoecious. Androecia on short, abbreviated, ventral-intercalary, spicate branches from main shoot or short- to long-flagelliform branches that are often copiously produced toward the shoot base; bracts closely imbricate, dorsally assurgent, deeply concave, 2–3-lobed to ca. 0.5, the lobes terminating in a uniseriate row of 2–3 cells, the terminal cell tapering to a rounded summit; dorsal margin of lamina not dilated, entire or with a tooth toward base; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent. Gynoecia on reduced ventral-intercalary branches from main axis or short ventral-intercalary, flagelliform branches that are often copiously produced, the mature gynoecium with bracts rather large for perianth size, those of innermost series concave to ± canaliculate, broadly ovate, 2–4-lobulate, the armature narrowly acute to short-acuminate, terminating in 2 laterally juxtaposed cells or, more often, a single cell or a uniseriate row of at most 2(3) somewhat elongated cells, often with a terminal slime papilla; lamina composed of ± regularly subrectangular cells, the margins curved, subentire or sparingly crenate by the divergent apical or free end of marginal cells; bracteoles similar in form and size to bracts, or slightly smaller. Perianth long-emergent, fusiform to long and narrowly subclavate, terete in basal sector, obscurely trigonous above, the perianth narrowing toward the contracted mouth; mouth crenate-denticulate by the variably free tips of the thin-walled marginal cells, at times with 1 or a few processes with a complete cell laterally free and its supporting cell free by ca. 0.5.

Seta with 8 rows of outer cells surrounding an inner core of 12 much smaller cells. Capsule long-ellipsoidal, 23–26 μm thick, of 3 layers, the outer layer equivalent to the combined thickness of the two inner layers; outer layer of cells (surface view) in ± tiers, thin-walled, short-rectangular, with two-phase development, the longitudinal walls with moderately thickened continuous sheets of pigmented material and rather weakly developed nodule-like thickenings (lending a sinuous appearance to the longitudinal walls) alternating with walls that are devoid of thickenings, the transverse walls also devoid of thickenings; innermost layer of cells somewhat irregularly narrowly rectangular, the radial walls with thin but continuous sheets of wall material, the radial walls mostly with nodular thickenings and short spine-like extensions onto the exposed tangential wall, only exceptionally with complete semiannular bands.

Spores 11–12.5 μm in diam., the wall red-brown, with a network of low but sharply defined vermiculate markings that coalesce to delimit areolae. Elaters ± rigid to feebly sinuous, 8.6–9.6 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–3.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: Campbell Island, Stewart Island (5 m), South Island (25–630 m), North Island (600–900 m), Chatham Islands. Known from Otago (Dart River), Westland (Lake Kaniere, Nelson Lakes Natl. Park), Western Nelson (Punakaiki), Taranaki (Mt. Taranaki) and Northland (Waipoua) EPs.

Widespread but sporadic. On Stewart Island (track to Mason Bay) the species was found near sea level on sandy soil under a ledge of a small bank at the track margin in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath (to 1–

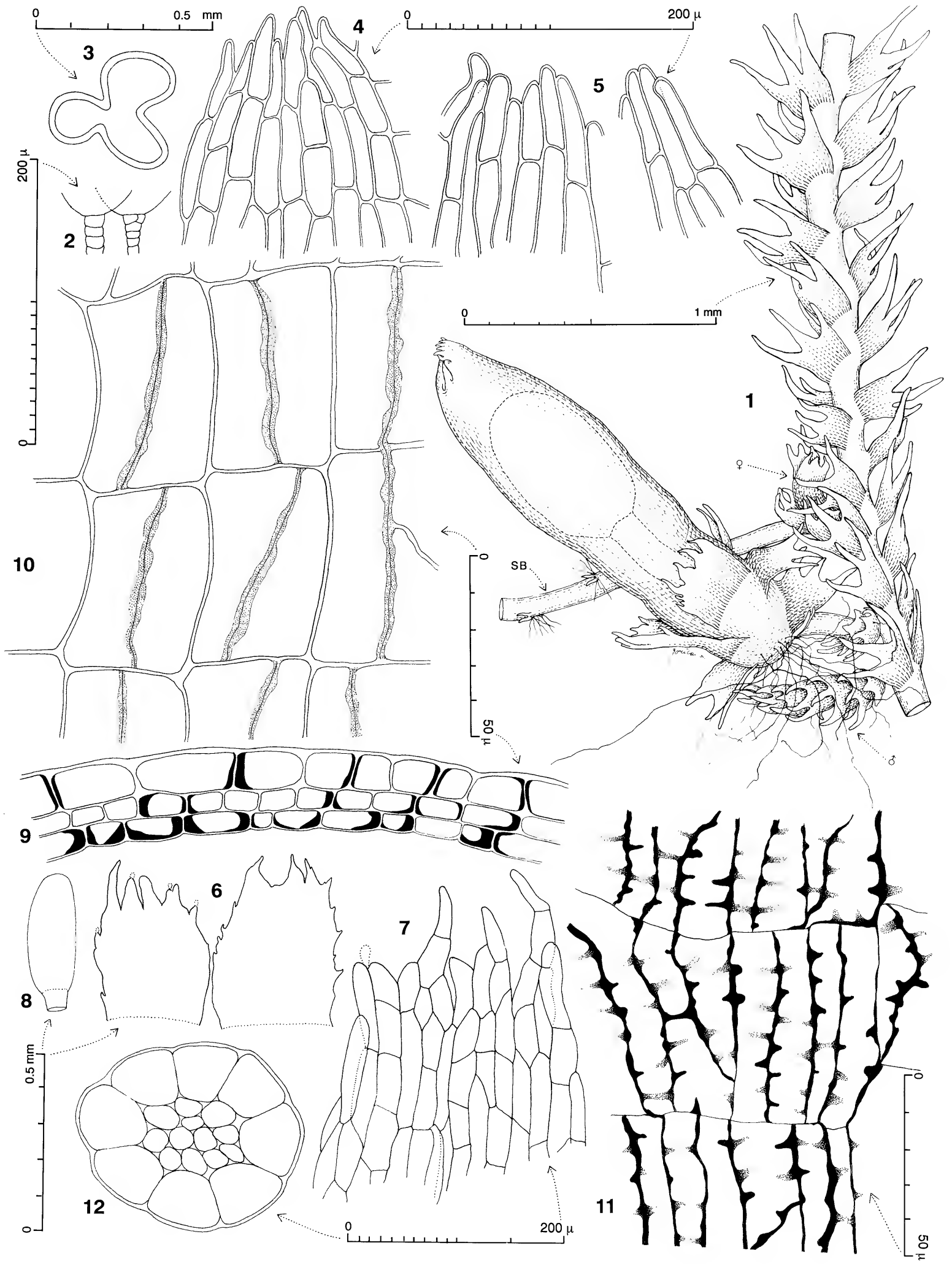

Fig. 72.
Telaranea martinii (E.A.Hodgs.) R.M.Schust. 1. Plant showing monoecious condition (♂ = androecium; ♀ = unfertilized gynoecium; SB = stoloniform branch), dorsal view. 2. Antheridium. 3. Perianth, cross section through distal sector. 4, 5. Portion of perianth mouth. 6. Innermost ♀ bracts. 7. Distal sector of ♀ bract. 8. Capsule profile. 9. Capsule wall, cross section. 10. Capsule wall, outer layer. 11. Capsule wall, inner layer. 12. Seta, cross section. (Figs. 1, 3, 5–7, 9–12, from

2 m tall) and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. The species in general occurs at lower elevations in the South Island. At Cascade Road (South Westland, 45 m) it occurred under the lip of projecting rock on a large vertical roadside bryophyte-covered bank at the margin of mature *Nothofagus menziesii* forest. It is also found on vertical banks (e.g., at the forest edge near the margin of Lake Kaniere) as well as on roadside banks. It is also present over limestone outcrops and cliffs in a mixed broadleaf forest (Bullock Creek, Punakaiki, Western Nelson EP, 25 m). In the Rotoiti–Rotoroa lakes area (Nelson Lakes Natl. Park, 630 m) the species forms solid yellow-green mats in sheltered niches of stream banks in forests dominated by *N. menziesii*. It is also on silty banks in the Dart Valley. The species also occurs on roadside banks in the North Island, but at higher elevations (610–915 m, type).

Comments: Several notable features characterize this species. Plants consistently have 3-lobed stem leaves, undivided half-leaves (Fig. 71: 1), and asymmetrically bifid first branch underleaves, with one lobe resembling a leaf lobe and the other shorter and ending in a slime papilla, thus resembling a normal underleaf lobe (Fig. 71: 6). *Telaranea martinii* is also monoecious (Fig. 72: 1), the only bisexual species in our area.

For comments on reproductive biology see Engel and Merrill (2004).

Telaranea nivicola R.M.Schust.

Telaranea nivicola R.M.Schust., Nova Hedwigia 15: 460. *pl. 52*. 1968. Holotype: New Zealand, South Is., above Sealy Lakes, Sealy Ra., Mt. Cook Natl. Park, ca. 5500 ft., *Schuster 67-491b* (F).

Plants very delicate (leaf cells collapsing in drying), lax, light or clear green, whitish with age, rather nitid to glistening; shoots 670–800 μm wide with leaves. Branching rather common, irregular, of the *Frullania* type; branch half-leaf often dorsally assurgent, undivided, biseriate at base; first branch underleaf on ventral-lateral side of branch somewhat above its base, often strongly asymmetric, one segment leaf-lobe-like and 4–5 cells long, the other consisting of a single elongated cell with several small rhizoid initial cells at its base, ending in a slime papilla, or aborted. Ventral-intercalary branches at least as common as terminal branches. Stems rather succulent in appearance, with 9–10 rows of large, delicate, leptodermous, cortical cells (being ca. 3.5–4× the radial diam. of medullary cells); medulla with (14)18–24 rows of small cells. Leaves distant, transverse to feebly incubous, (230)365–415 μm long, asymmetric, with the ventral lobe of 3-fid leaves smaller, (2)3-fid on leading stems (the basal cell pairs connate for up to 0.5 their length, forming a vestigial disc 4–6 cells broad). Lobes acuminate, strongly tapered, broadly incurved, consisting of a basal pair of distinctly elongate cells and a uniseriate row of 3–4 cells (rarely biseriate for an additional tier above base), the dorsal lobe(s) usually somewhat longer, the ventral lobe of 3-fid leaves at times uniseriate to base. Cells large, turgid and barrel-shaped, the paired basal cells approaching 0.5 the length of lobe, ca. 38–40 μm wide × 85–120 μm long to 50–55 μm wide × 150–180 μm long; first cell of uniseriate segment 26–40 μm wide × 66–86 μm long to ca. 36–55 μm wide × 95–125 μm long, the terminal 1–2 cell(s) much shorter and strongly

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Child 2009, New Zealand, South Is., Westland EP, Paradise, Dart Valley; 2, 4, 8, from type of *Lepidozia martinii*.)

tapering to a rounded tip; cells thin-walled but firm, the transverse septa constricted; surface smooth. Oil-bodies (*fide* Schuster, 1968b) colorless, ± homogeneous but not strongly glistening, fusiform to ellipsoidal to crescentic-fusiform, (4)5–9(10) per cell (except in small 1–2 distal cells), mostly 1.5–2 × 3–6 μm to 2.2 × 2.8–3.5 μm up to 1.5–1.8(2) × 6.5–8 μm. Underleaves small and inconspicuous, 3–4-fid; lobes usually 1–2-celled, terminating in a slime papilla, the basal cells of lobes distinctly elongated (to 3:1), inserted on a pair of laterally juxtaposed cells or with secondary divisions resulting in a disc-like tier of small, quadrate, rhizoid initials. Asexual reproduction lacking.

Androecia not seen. Gynoecia (see Schuster, 1968b, fig. 52: 1, ♀ bracts).

Distribution and Ecology: Endemic to New Zealand: South Island (1435 m), North Island (1370 m). Known from Westland (Mt. Brewster), Canterbury (Sealy Ra.) and Southern North Island (Ruahine Ra.) EPs.

Known only from a few widely scattered sites. The type occurred amidst *Allisonia cockaynei*, *Austrolophozia paradoxa*, *Chiloscyphus cuspidatus*, *Isotachis lyallii* and *Phyllothallia nivicola* on dead *Chionochloa* culms. The plant also occurs in the penalpine tussock zone at ca. 1435 m on Mt. Brewster and was removed from mats of *Allisonia cockaynei*, intermingled with *Diplophyllum domesticum*, *Isotachis lyallii*, *Metzgeria furcata*, *Phyllothallia nivicola*, *Solenostoma rufiflorum* and *Telaranea quadriseta*. Also known from two stations in the Ruahine Ra., both in the Whanahuia Ra.; one of these occurred in boggy areas at 1370 m on Mt. Mangahuia.

Comments: A distinctive species, very similar to *Telaranea pseudozoopsis* (Herzog) Fulford of southern South America, the Falkland Islands and Juan Fernandez. Both have leaf lobes of somewhat turgid cells, constricted at the septa, with marked and progressive reduction in cell size from lobe base to apex. Both species have 2- to 3-fid stem leaves. However, *T. pseudozoopsis* has a distinct disc formed of a single cell tier of slightly elongated cells, smaller than the basal lobe cells. It also has a cortex of immense inflated cells and the underleaves are apparently always 2-lobed, vs. 3–4-lobed in *T. nivicola*.

This species resembles a small version of *Telaranea remotifolia*, in its rather flaccid, sinuous, loosely matted stems, and the leaves shrunken and inconspicuous when dry. The plants have a iridescent, glass-like appearance when dry.

Telaranea granulata J.J.Engel & Merrill

[Fig. 73]

Telaranea granulata J.J.Engel & Merrill, Fieldiana, Bot. 44: 103. *f. 31*. 2003. Holotype: New Zealand, North Is., North Auckland Prov., Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waiotemarama Track, 650–680 m, *Engel 22594* (F).

Plants exceedingly delicate, thread-like, minutely prickly, appressed, epiphyllous on fern leaves, pale green, highly nitid; shoots minute, to 525 μm wide with leaves. Branching distantly and somewhat irregularly 1-pinnate, the branches of *Frullania* type, the main axis terete, the branches dorsiventrally flattened; branch half-leaf undivided, occasionally bilobed; first branch underleaf consistently undivided, inserted on median ventral base of branch, biseriate at base, with a uniseriate row 2–3 cells long (or uniseriate throughout), terminating in a slime

papilla. Ventral-intercalary branches occasional, at times becoming leading shoots. Stems slender, the cortical cells distinctly differentiated, thin-walled but firm, in 12 rows, in section somewhat larger than the medullary cells; medullary cells in 16 rows. Main shoots with 3–4 cortical cells intervening between successive leaves on either side, the branches with 2 (rarely 3) cells intervening between successive leaves on either side of branch. Leaves on main shoot rather distant, stiffly spreading, lending the stem a prickly aspect, the insertion weakly incubous to subtransverse, 390–495 μm wide (at tips of spreading lobes) × 245–310 μm long, deeply 3-lobed (4-lobed only on strongest shoots). Branch leaves 3-lobed, closely imbricate, the insertion moderately incubous, the insertion narrowly impinging on the 2 median rows of cortical cells, leaving a ± evident median strip along the dorsal side of the branch. Lobes ± equal in length, gradually tapering from base to apex, broadly incurved, moderately to widely divergent, from a biseriate base (at times with an additional biseriate tier), the uniseriate row 4–5 cells long; lobe cells thin-walled, the transverse septa at most feebly thickened in the corners, the lobes constricted at the septa; surface minutely scabrous. Disc 6 cells wide (8 in 4-lobed leaves); 2 cells high (1.5 cells high, the lobe bases connate for 0.5 or as little as 0.3 their length), consisting of a single tier of cells along the insertion, plus the paired basal cells of the lobes; basal tier of disc cells often incomplete, not extending to one or both margins, the disc then 0.5 cells high at margins. Cells of disc subquadrate, 13–19 μm wide × 24–36 μm long; surface smooth. Underleaves approaching the leaves in size, symmetrically 3-lobed (4-lobed on strongest shoots), the disc consisting of the partially connate basal cell pairs of the lobes; lobes biseriate at base, with a uniseriate row of 3(4) elongate cells (the distal cell shorter and often hooked), ending in a slime papilla. Rhizoids, when present, arising from swollen cells produced by vertical division of basal cell pairs, the disc then appearing bistratose in part.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: North Island (650–680 m), Three Kings Islands. Known only from two specimens. The type is from a wind-pruned scrub consisting of *Coprosma grandifolia*, *Melicytus ramiflorus* and *Olearia rani* at 650–680 m. Plants occurred epiphyllous on *Hymenophyllum* sp. on a deeply shaded log with other filmy ferns. The Three Kings Islands specimen occurred on rock in a stream shaded by *Kunzea* canopy, growing with *Distichophyllum*, *Balantiopsis*, *Leiomitra lanata* and *Riccardia*.

Comments: This species is unusual for its deeply divided, 3-lobed leaves (Fig. 73: 1, 3), conspicuously flattened branches, minutely scabrous surface (Fig. 73: 9) and large, 3-lobed underleaves, which are subequal to the leaves in size (Fig. 73: 3). The branch leaves are widely set, leaving the two dorsal rows of cortical cells broadly exposed (Fig. 73: 5). *Telaranea lindenbergii* var. *complanata* of New Zealand has complanate-foliate branches that appear comb-like, a result of the obliquely spreading, incubously oriented branch leaves. The branch leaf insertions, however, approach the midline of the branch, without leaving a conspicuous median strip.

Several other Australasian species of *Telaranea* have 2–3-lobed, deeply divided leaves. In *T. herzogii* the leaf "disc" is formed from the cells of the partially connate lobe bases, lacking a tier of disc cells along the insertion. In *T. granulata*, there is at least one complete tier of disc cells along the insertion, plus the basal cells of the lobes. *Telaranea trilobata* and *T. fragilifolia* have similar leaves but produce *Microlepidozia*-type branches, which are unknown in *T. granulata*. In addition, the leaf lobes of *T. fragilifolia* are caducous.

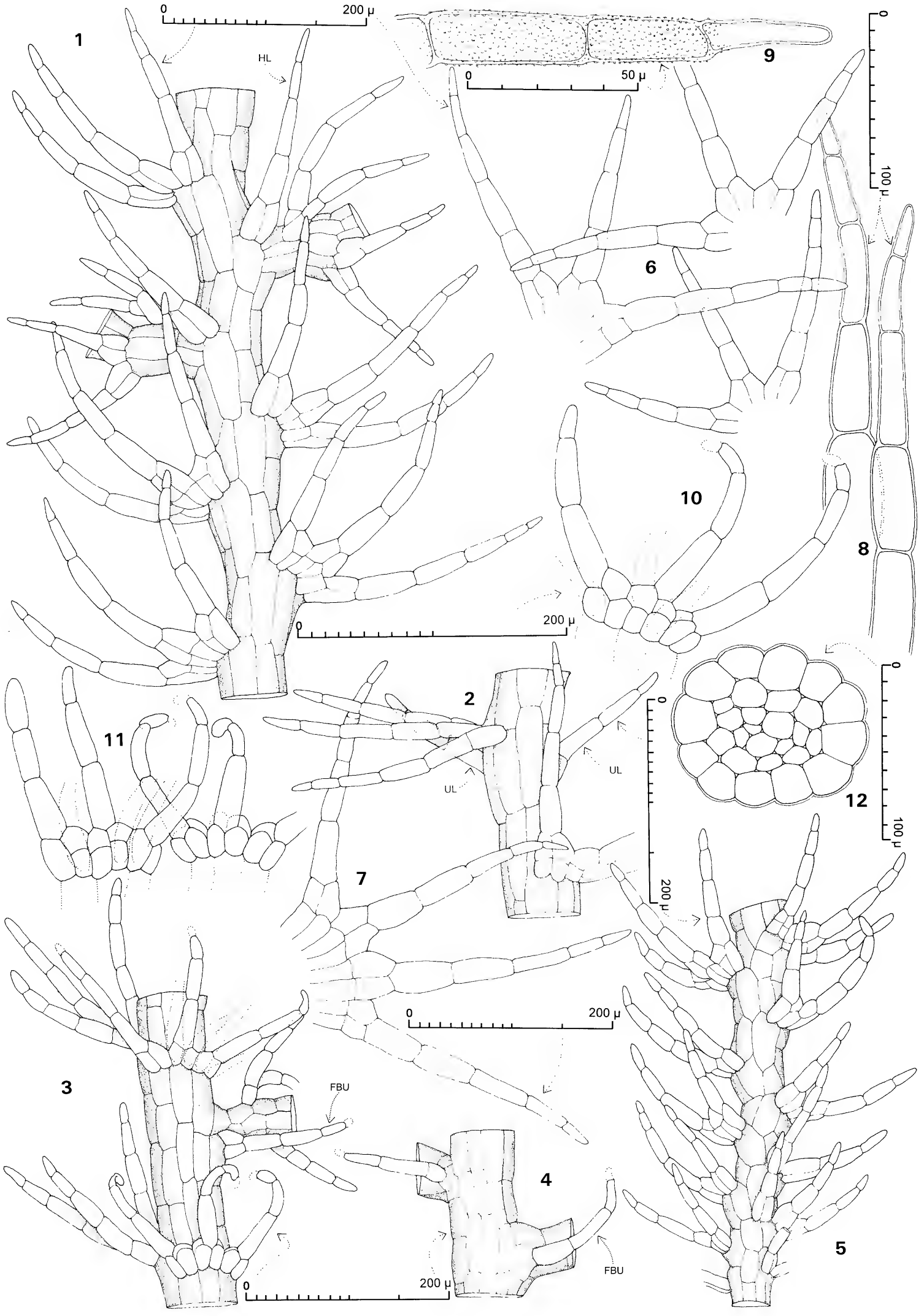

Fig. 73.
Telaranea granulata J.J.Engel & Merrill. 1. Portion of main shoot with base of *Frullania*-type branch, dorsal view; note 3 stem cortical cells between leaves, undivided half-leaf (= HL), and variation in disc of main axis leaves. 2. Portion of main shoot, dorsal view; note that portions of

Telaranea quinquespina (J.J.Engel & Merrill) J.J.Engel & Merrill
[Fig. 74]

Kurzia quinquespina J.J.Engel & Merrill, J. Hattori Bot. Lab. 80: 217. *f. 1*. 1996. *Telaranea quinquespina* (J.J.Engel & Merrill) J.J.Engel & Merrill, Fieldiana, Bot. 44: 109. 2004. Holotype: New Zealand, South Is., Buller Co., gorge of Bullock Creek, 1.2 miles E of Rte. 6, 100 ft., *Fife 4720* (F); isotype: (CHR).

Plants delicate, loosely to densely caespitose in felt-like mats (or creeping as individual strands among other bryophytes), minutely prickly in appearance, pale green, nitid; shoots minute, to 845 μm wide with leaves. Branching sparing to rather common, irregular, with *Frullania*- and *Microlepidozia*-type terminal branches and ventral- and lateral-intercalary branches; terminal branches with half-leaf undivided and setaceous (rarely bifid), biseriate in basal tier (occasionally with a second biseriate tier), the uniseriate row of 4–5 cells; first branch underleaf on base of branch, symmetrically bilobed, resembling a leaf but with shorter lobes, the uniseriate row 4 cells long (rarely asymmetrically bilobed and resembling the stem underleaves); ventral- and lateral-intercalary branches frequent, often becoming leading, leafy shoots; leafless geotropic ventral-intercalary and lateral-intercalary stolons frequently present. Stems slender, delicate and thread-like, the cortical cells in 6(7) rows, the outer wall thicker-walled; medullary cells much smaller in diameter than the cortical cells, in (3)4–5 rows. Leaves contiguous to laxly imbricate, widely spreading, the insertion transverse or nearly so, 230–450 × 220–365 μm (between tips of spreading lobes), bifid almost to the base (the basal cells connate for 0.3 to 0.5 their length), occasionally 3-lobed. Lobes ± equal in length, stiff, subcapillary, gradually tapering from base to apex, straight to broadly curved, widely divergent, biseriate at the base (at times uniseriate to base on some shoots), with a uniseriate row of (4)5–6(7) cells; cells of basal tier (13)17–24 μm wide × 42–62 μm long, basal cell of uniseriate row 15–25 × 55–96 μm, the next cell of about the same length and width, the terminal cell distinctly shorter than the penultimate cell, at times appearing secondarily divided; cell walls firm, moderately thick-walled, the transverse septa of uniseriate row thickened in the corners and swollen to weakly projecting; surface smooth. Underleaves asymmetrically bilobed, consisting of a longer lobe that is biseriate at the base and ending in a uniseriate row of 4(5) cells, thus resembling a leaf lobe, the other lobe abbreviated, consisting of a pair of short basal cells and a ± elongated distal cell, terminating in a slime papilla, the underleaves occasionally 3-lobed, with middle lobe abbreviated, or sporadically with 2 abbreviated lobes; paired cells at base of the shorter lobe(s) at times transversely divided, with rhizoids produced from the resulting rhizoid initials. Asexual reproduction lacking.

Plants dioecious. Androecium on a short, determinate, lateral-intercalary branch from main shoot, loosely spicate; bracts concave, 3-lobed to ca. 0.65, the disc 1(2) cells high, the lobes

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underleaf (= UL) are visible. 3, 4. Portions of main axis and base of *Frullania*-type branch, ventral view; note (left) first branch underleaf (= FBU) is biseriate at base or (at right) uniseriate throughout (rhizoids indicated with stipple). 5. Portion of primary branch, dorsal view. 6, 7. Three- and 4-lobed leaves of main shoot (all drawn to same scale). 8. Leaf lobes, the surface detail not shown. 9. Apical portion of leaf lobe, the surface detail shown in part. 10, 11. Underleaves, the underleaf at right in fig. 11 with rhizoid initials formed but lacking rhizoids, the other underleaves with rhizoids shown in stipple (all drawn to same scale). 12. Stem of main shoot, cross section. (All from holotype.)

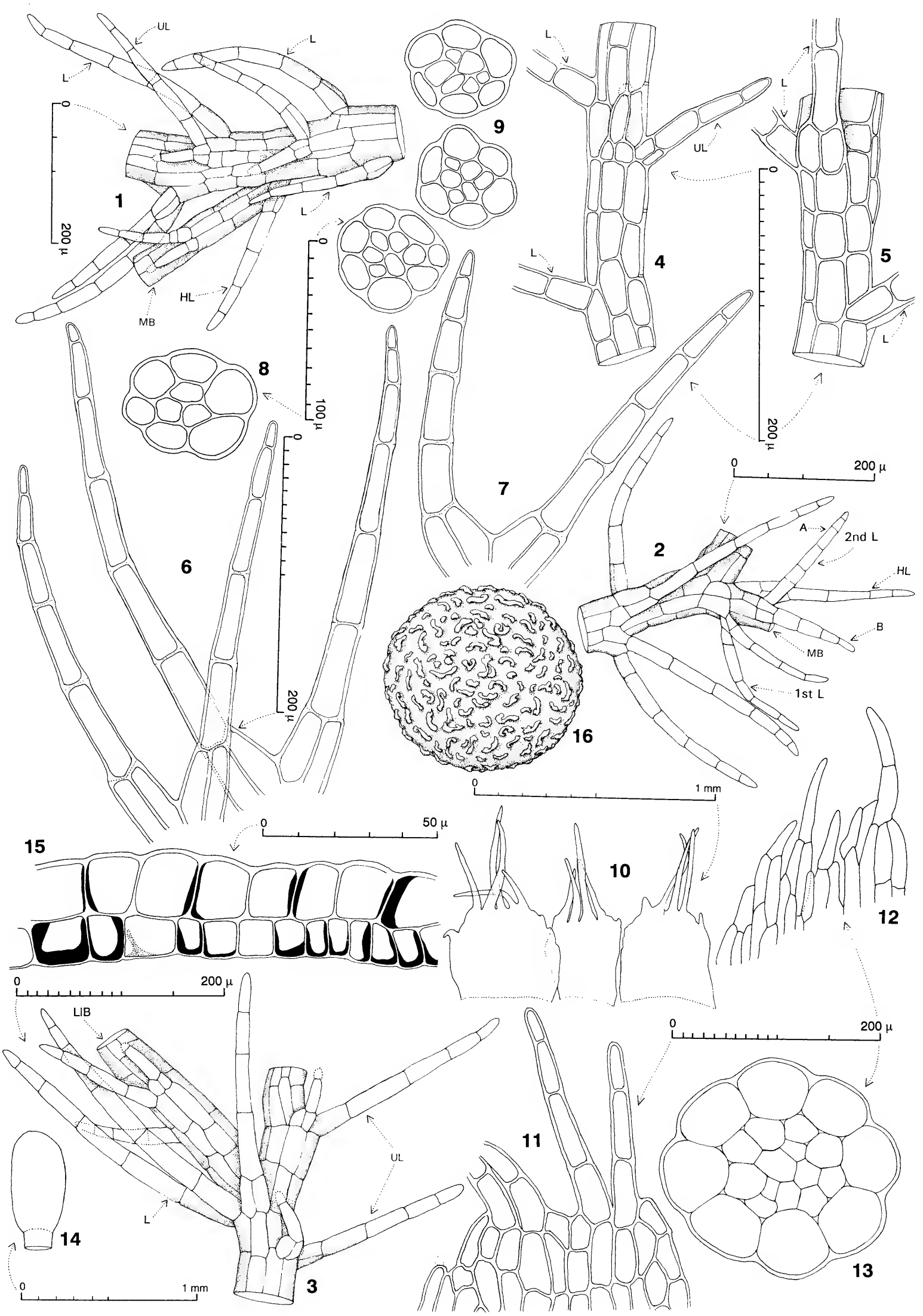

Fig. 74.
Telaranea quinquespina (J.J.Engel & Merrill) J.J.Engel & Merrill. 1. Portion of main shoot with *Microlepidozia*-type branch (= MB), ventral view (L = leaf; UL = underleaf; HL = half-leaf). 2.

2–3 cells wide at base, slenderly tapering, terminating in a uniseriate row of up to 4 cells; antheridia 1 per bract, the stalk uniseriate. Gynoecia on short, ventral- and lateral-intercalary branches from main shoot; innermost bracts and bracteole similar, the disc subquadrate, ± regularly (3)4(5)-lobed to 0.4 (often bisbifid, the lobes in pairs), the lobes ciliiform, uniseriate or 2 cells wide at extreme base, the uniseriate row of 3–4 cells (4 when uniseriate to base), the disc margins with several small blunt teeth. Perianth terete in basal half, tapering to the strongly plicate, shallowly lobulate-ciliate mouth, the divisions ca. 9, acuminate, 2–4 cells wide at base, ending in a single, elongate, blunt-tipped cell or uniseriate row of 2 elongate cells, the margins of divisions weakly dentate by projecting ends of cells.

Seta with 8 rows of larger epidermal cells surrounding an inner core of 10–12 much smaller cells. Capsule oblong-ellipsoidal, the wall 28–36 μm thick, 2(locally 3)-stratose, the outer layer subequal to the inner or slightly thicker (the inner layer thinnest in 3-stratose portions); outer layer of cells distinctly tiered, ± regularly short-rectangular, with two-phase development, the radial longitudinal walls with rather thin, pigmented, sheet-like thickenings that are sinuate or with local, pigmented, nodular swellings (2–4 per cell), alternating with primary walls devoid of thickenings, the transverse walls without thickenings; inner layer of cells narrowly rectangular, with semiannular bands frequent, widely spaced, complete or less commonly incomplete and then extending onto the tangential wall as spine-like extensions or nodular swellings.

Spores 14.4–19.2 μm in diam., the wall pale reddish brown, with distinct, low, rough papillae, often coalescing into short ridges that do not anastomose to form areolae. Elaters somewhat twisted, 8.2–9.1 μm wide, slightly tapering, bispiral to tips, the spirals 3.4 μm wide.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5 m), South Island (135 m), North Island (60–1080 m). Known from Westland, Volcanic Plateau (Tongariro Natl. Park, Atiamuri), Gisborne, Auckland (Kaimai Ra., Coromandel Peninsula) and Northland EPs.

Known from few and scattered localities. *Telaranea quinquespina* for the most part occurs loosely in damp, shaded niches on steep-sided banks, bryophyte-covered tree bases, cliff faces and stream banks in lower- to middle-elevation forests. The species appears to grow in at most moderately shaded conditions and may even tolerate relatively open situations (Cascade ultramafic moraine). The Stewart Island as well both South Island stations are at lower elevations. On Stewart Island the species occurred near sea level in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. At this site the species formed a loose intertwined layer below the surface litter. The type (Bullock Creek gorge, Punakaiki, 30 m) occurred on a weakly shaded limestone face with *Adiantum* and *Coprosma* at the margin of a

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Portion of main shoot with *Microlepidozia*-type branch (= MB), dorsal view (1st L = first leaf; 2nd L = second leaf, with lobes A + B; HL = half-leaf on opposing side of stem). 3. Portion of main shoot with lateral-intercalary branch (= LIB) in axil of 3-lobed leaf (= L), ventral-lateral view (UL = underleaf). 4. Stem, ventral aspect (L = leaf; UL = underleaf). 5. Stem, dorsal aspect (L = leaf, at top the 2 lobes shown at arrows). 6, 7. Leaves. 8, 9. Stem, cross sections. 10. Innermost ♀ bracts and bracteole. 11. Distal sector of innermost ♀ bract. 12. Portion of perianth mouth. 13. Seta, cross section. 14. Capsule profile. 15. Capsule wall, cross section. 16. Spore (× 1552). (Figs. 1, 2, 4–6, 9, from *Engel 21201*, New Zealand, North Is., Volcanic Plateau EP, Tree Trunk Gorge, W bank of Tongariro R., E border of Tongariro Natl. Park; 3, from *Engel 21202*, same loc.; 7, 8, 10–16, from isotype.)

vehicle track. In Westland (Cascade Road, 135 m), in an area of ultramafic rocks and outcrops with rather open vegetation consisting mainly of *Gleichenia*, *Lycopodiella*, *Baumea*, the lichen *Cladonia* and scattered *Leptospermum scoparium*, the species occurs terricolous on slopes with *Kurzia hippuroides*. At the northernmost station (Radar Bush near North Cape at 34° 28.5′ S) the species occurs on very thin soil over rock of a bank above a stream at the bottom of a steep-sided valley within a forest of *Beilschmiedia – Vitex – Hoheria* and *Cyathea dealbata*. At the single higher-elevation forest locality (Mt. Ruapehu, Taranaki Falls track, 1080 m), the plants occurred over soil in a shaded pocket of a bank in a steep-sided canyon through forest of *Nothofagus solandri* var. *cliffortioides*, *Griselinia littoralis*, *Pseudopanax colensoi* and *Podocarpus hallii*.

Comments: *Telaranea quinquespina* resembles *T. herzogii* (p. 350), but can be readily distinguished by the biseriate tier of cells at the base of each lobe (Fig. 74: 6, 7). The leaf lobes of *T. herzogii* are typically uniseriate to the base (Fig. 75: 5, 6). In addition, the underleaves in *T. quinquespina* are asymmetrically bilobed (Fig. 74: 1, 3), with the stronger lobe remarkably similar to (and only slightly shorter than) the lobe of a leaf (Fig. 74: 4). Both ventral-intercalary and lateral-intercalary branches are frequently produced in *T. quinquespina*. Terminal, *Microlepidozia*- and *Frullania*-type branches are infrequently produced, but not in regular alternation on opposite sides of the stem as, for example, in *T. quadriseta*.

Sect. ***Tenuifoliae*** (R.M.Schust.) J.J.Engel & Merrill

Arachniopsis sect. *Tenuifoliae* R.M.Schust., Beih. Nova Hedwigia 118: 461. 2000. *Telaranea* sect. *Tenuifoliae* (R.M.Schust.) J.J.Engel & Merrill, Fieldiana, Bot. 44: 112. 2004. Type: *Arachniopsis tenuifolia* R.M.Schust.

Arachniopsis Spruce, Cephalozia 84. 1882.

Arachniopsis subg. *Amphidactylopsis* R.M.Schust., Nova Hedwigia 10: 25. 1965. Type: *Arachniopsis monocera* R.M.Schust. & Grolle, *nom. inval.*

Telaranea herzogii (E.A.Hodgs.) E.A.Hodgs.

[Plate 6B; Figs. 75, 76; Fig. 77: 2, oil-bodies, p. 355]

Lepidozia herzogii E.A.Hodgs., Trans. Roy. Soc. New Zealand 83: 618. 1956, *nom. nov. pro Lepidozia bisetula* Herzog *in* E.A.Hodgs., Trans. & Proc. Roy. Soc. New Zealand 68: 44. *pl. 5, d–f.* 1938, *non L. bisetula* Steph., Sp. Hepat. 6: 323. 1922. *Telaranea herzogii* (E.A.Hodgs.) E.A.Hodgs., Rec. Domin. Mus. 4: 106. 1962. *Arachniopsis herzogii* (E.A.Hodgs.) E.A.Hodgs., Tuatara 12: 6. 1964. Type: New Zealand, North Is., Russell, Bay of Islands, *Lindauer 281* (CHR!).

Telaranea exigua R.M.Schust., Nova Hedwigia 15: 457. 1968. Holotype: New Zealand, North Is., Mt. Egmont, along Stratford Mtn. Road, E side of mountain, ca. 2000 ft., *Schuster 48916b* (*non vidi*).

Plants exceedingly delicate, minutely prickly in appearance, creeping to ascending, whitish green and nitid; shoots minute, to 630 μm wide with leaves. Branching sparing to very common, irregular, not becoming flagelliform; branch half-leaf stiffly dorsally assurgent, undivided, setaceous; first branch underleaf at base of branch, strongly asymmetrically bilobed, consisting of a divergent lobe, (2)3–4 cells long and a ± appressed, curved lobe aligned with the branch, resembling an underleaf lobe and consisting of a short basal cell and a ± elongated

distal cell, the lobe terminating in a slime papilla, a rhizoid commonly originating from the basal cell. Ventral-intercalary branches occasional to predominant, long and leafy. Stems very delicate, rather stiff for plant size, the cortical cells in 6–9 rows, much larger than the medullary cells which are in 3(4) to 6–11(18) rows. Main shoots with 3–4 cortical cells intervening between successive leaves on either side, the branches with 2–3 cells intervening between successive leaves on either side of branch. Leaves rather rigid, contiguous to weakly imbricate (strongly imbricate on branches), widely spreading to subsquarrose, the insertion transverse to weakly succubous, (245)300–450(490) × 245–420 μm (at tips of spreading lobes), 2–3-fid almost to the base (the basal cells connate for 0.1–0.4 their length), the ventral lobe somewhat shorter. Lobes stiff, gradually tapering from base to apex, straight to broadly incurved, moderately to strongly divergent, on branches disposed in ± regular ranks, uniseriate throughout (sporadically one or more lobes biseriate at extreme base), gradually tapering, the lobes (4)5–6(7) cells long, ± equal in length, or in 3-lobed leaves the ventral lobe perceptibly shorter; basal cells 18–26 μm wide × (66)95–120 μm long, the next cell 14–20 × 56–98 μm; lobe cells gradually shorter and narrower distally, the terminal cell usually much shorter than the penultimate cell; cell walls thin but firm to moderately thick-walled, the transverse septa thickened in the corners and not or feebly swollen and projecting; surface smooth. Oil-bodies opaque, dull, greyish, (5)6–11 per basal cell of lobe, broadly elliptic to irregularly crescentic, often lumpy and irregular, very finely papillose, the globules imperceptibly bulging from membrane, oil-bodies 6.5 × 9 μm to 6–7 × 10–12 μm, less commonly spherical and 7 μm in diam., oil-bodies in second lobe cell 4–6 per cell, mostly spherical and 6–8 μm in diam. or nearly spherical and 7 × 8 μm; oil-bodies of stem cells much smaller and overall narrower, irregularly fusiform to linear to crescentic but with similar ornamentation to oil-bodies of leaves. Underleaves small and inconspicuous, 2(rarely 3)-lobed, caliper-like, the lobes parallel to somewhat divergent, 2–3 cells long (rarely 1 cell), terminating in a hooked slime papilla, the base formed of 2 basally connate, curved cells forming a U-shaped disc, the distal cell(s) elongated; individual rhizoids originating from the base or apex (rarely both) of the basal lobe cells, or the basal cells subdivided into 6–8 small, quadrate, rhizoid initials, with a rhizoid emerging from each. Asexual reproduction lacking. Fungal partner an ascomycete.

Plants apparently dioecious. Androecia not seen. Gynoecial bracts delicate, deeply dissected, 2–3-lobed, the lobes 2–4 cells wide at base, terminating in a uniseriate row of 5–6 elongated, tapering cells, each lobe armed with paired uniseriate cilia inserted at apex of the basal tier of lobe cells, the cilia 2–4-celled, often ending in a slime papilla; disc of 2(3) tiers of longitudinally elongate cells, the margins of disc entire or with a blunt tooth on one or both sides at base of the lateral lobes; bracteoles 2-lobed, otherwise similar to bracts. Perianth rather short, terete in basal half, bluntly trigonous above, somewhat contracted at the mouth, the mouth shallowly lobulate-ciliate, the cilia ca. 6–10 (interspersed with smaller 1–2-celled teeth), several cells wide at the extreme base, ending in a stiffly divergent uniseriate process of 4–9 elongate cells, the cilia often armed with few-celled lateral spurs or a single lateral spur inserted at the septa.

Seta with 8 rows of outer cells surrounding an inner core of 4–10 much smaller cells. Capsule rather short- to long-ellipsoidal, 190 μm wide, 345 μm long, the wall 16–18 μm thick, uniformly 2-stratose, the outer layer subequal to the inner, or slightly thicker; outer layer of cells ± regularly short-rectangular, with two-phase development, the longitudinal walls with nodule-like thickenings (4–6 per cell) alternating with primary walls devoid of thickenings (or rarely with local, pigmented, nodular swellings), the transverse walls without thickenings; innermost layer of cells somewhat irregularly narrowly rectangular, the radial walls with

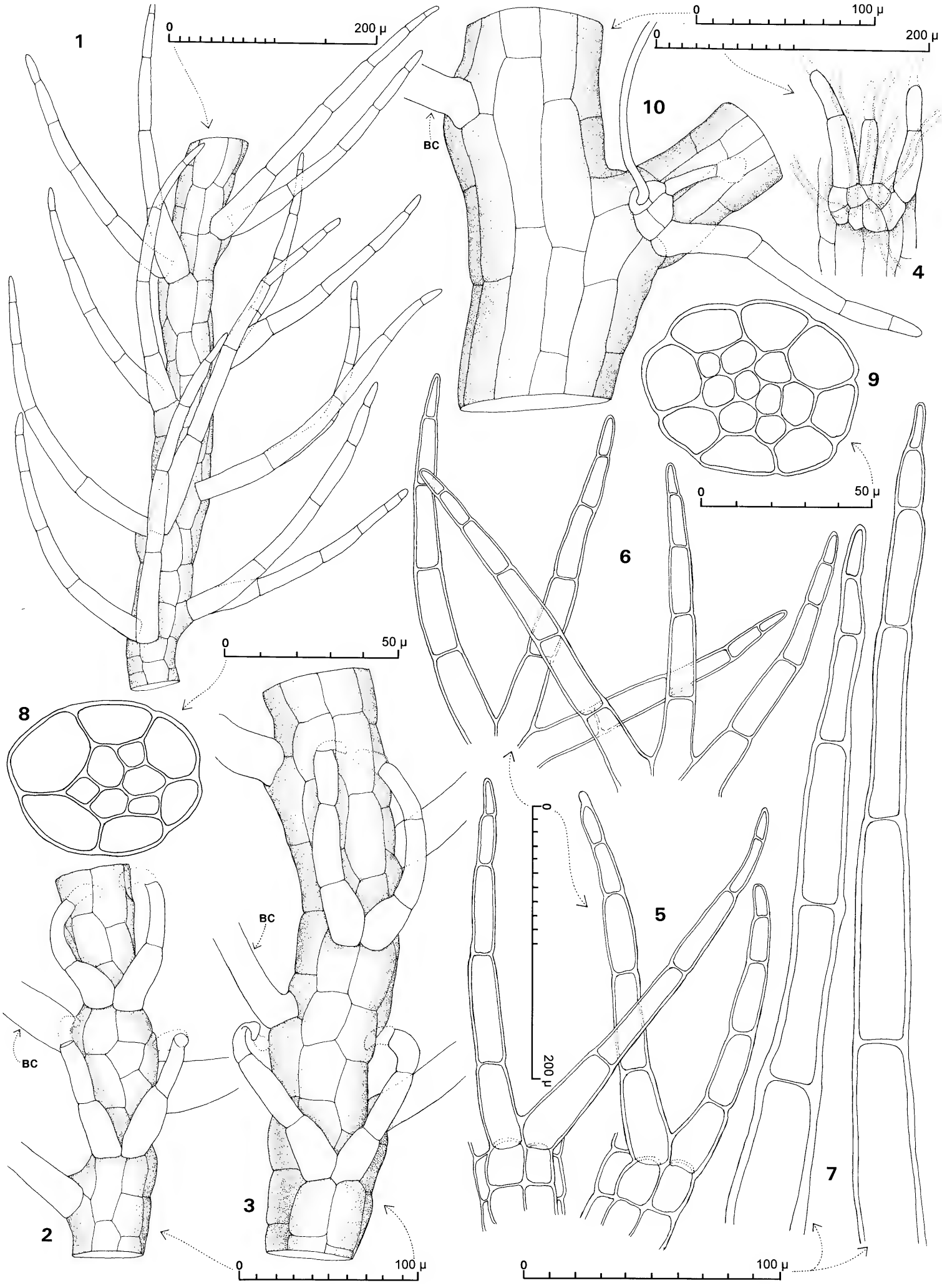

Fig. 75.
Telaranea herzogii (E.A.Hodgs.) E.A.Hodgs. 1. Portion of main shoot, dorsal view. 2, 3. Portions of 2 different main shoots, each showing 2 underleaves and the basal cells of ventral lobes of 3 leaves (= BC), ventral view. 4. Three-lobed underleaf; note rhizoids (stippled outline). 5, 6. Two- and 3-lobed leaves. 7. Leaf lobes. 8, 9. Stem, cross sections (note 6 + 6 and 8 + 9 anatomy). 10. Terminal branch base and first branch underleaf (ventral view); note rhizoid position and rhizoid

continuous sheets of wall material, the radial walls mostly with nodular thickenings and short spine-like extensions onto the exposed tangential wall, only exceptionally with complete semiannular bands.

Spores 7.5–8.8 to 10.6–12 μm in diam., the wall yellow-brown, rather thin-walled, areolate, with a low, close network of ridges coalescing to delimit areolae. Elaters rather straight, 6.5–7.5 to 9.6–11 μm wide, only slightly tapering and bispiral to tips, the spirals 2.9–3.4 μm wide.

Distribution and Ecology: New Zealand: Stewart Island (20–200 m), South Island (10–890 m), North Island (25–890 m); Australia: Tasmania, Victoria. In New Zealand known from Fiordland, Southland, Otago, Westland, Canterbury (Arthur's Pass), Western Nelson, Southern North Island, Volcanic Plateau, Auckland and Northland EPs.

In New Zealand the species is found rather commonly on loamy, moist, shaded soil. It occurs for the most part in lower- to middle-elevation moist or swampy forests where it is on soil in protected pockets or shaded hollows associated with, for example, *Acromastigum colensoanum*, *Bazzania nitida*, *Lepidozia digitata*, *Riccardia colensoi, Saccogynidium australe*, *Telaranea elegans*, *T. tetradactyla*, *T. tetrapila* and *Zoopsis leitgebiana.*

It may occur over soil of the forest floor deep in humid recesses formed by rock ledges (e.g., Lake Marion, Fiordland) or it may form a loosely creeping, pure, felt-like covering over soil deep in pockets at tree bases (e.g., Hauturu Highpoint Track, Little Barrier Island). It is rather frequent in humid sites such as steep-sided stream banks and occurs loosely over soil in protected niches; in particularly humid sites it may be epiphyllous on filmy ferns such as *Trichomanes elongatum*. Also in moist, dense, tree-fern gullies, where *Telaranea herzogii* may be terricolous or on tree-fern caudices (of *Cyathea dealbata* or *Dicksonia squarrosa*). It also may be encountered rather commonly in cushions of *Leucobryum candidum*. It is much less frequent at higher elevations, as in the Temple Basin ski area (Arthur's Pass).

Comments: The delicate, densely interwoven, prickly and highly nitid shoots of *Telaranea herzogii* lend this species a distinctive appearance. The leaf lobes are uniseriate throughout (or sporadically biseriate at the base) and the basal cells are barely united, forming a "disc" of considerably less than one cell high (Fig. 75: 5, 6). In this connection it should be noted that the plant illustrated by Schuster (1969c, p. 33, fig. 88: 4–6) as *T. herzogii* is, in fact, *T. inaequalis*. The leaf lobes of *T. inaequalis* are rather flexuous, show essentially no taper and are unequal in length (Fig. 78: 4), the longest up to 9 cells long, and the lobe cells are of roughly equal length throughout. The leaves of *T. herzogii* are also ± asymmetrical, but the lobes are stiffly spreading and distinctly tapering, usually 5 (rarely 6) cells long (Fig. 75: 1, 5–7), the cells progressively narrower and shorter from base to apex (Fig. 75: 7). The first branch underleaves of *T. inaequalis* are equally bilobed like the other stem underleaves (Fig. 78: 3) vs. asymmetrically bilobed in *T. herzogii* (Fig. 75: 10).

Plants of *Telaranea herzogii* resemble those of *T. quinquespina*, but the latter can be readily distinguished by the combination of *Microlepidozia*-type branching, slender thread-like

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initial cells (BC = basal cell of ventral lobe of leaf). (Figs. 1–3, 5, 7, 8, from type of *T. herzogii*; 4, 6, 9, from *Engel 19239*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., upper slopes of N side of Tiropahi or Four Mile R.; 10, from *Engel 17968*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, summit area of Haast Pass.)

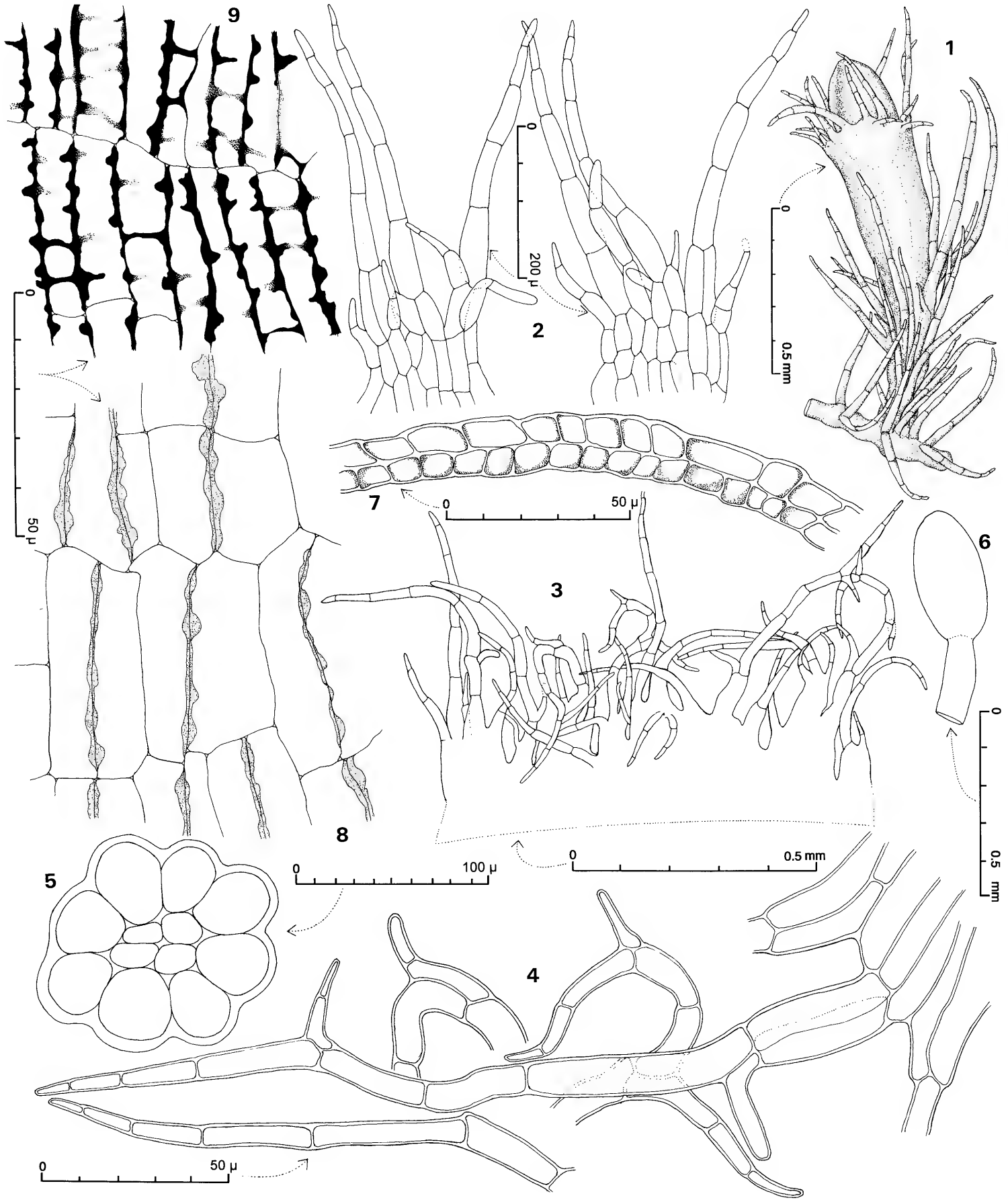

Fig. 76.
Telaranea herzogii (E.A.Hodgs.) E.A.Hodgs. 1. Gynoecium with mature sporophyte. 2. Innermost ♀ bracts. 3. Perianth mouth. 4. Cilia of perianth mouth. 5. Seta, cross section. 6. Capsule profile. 7. Capsule wall, cross section. 8. Capsule wall, outer layer. 9. Capsule wall, inner layer. (All from *Allison 3171*, New Zealand, North Is., Volcanic Plateau EP, near Atiamuri, S of Rotorua.)

stems, firm-walled cortical cells (Fig. 74: 8, 9), a biseriate tier of cells at the base of each leaf lobe (Fig. 74: 6, 7) and asymmetrically bilobed underleaves (Fig. 74: 1), the larger lobe similar to (and only slightly shorter than) the lobe of a leaf (Fig. 74: 4). The first branch underleaf of *T. quinquespina* is also unusual in being symmetrically bilobed and resembling a leaf; in *T. herzogii* it is asymmetrically bilobed, with one lobe much shorter and ending in a slime papilla.

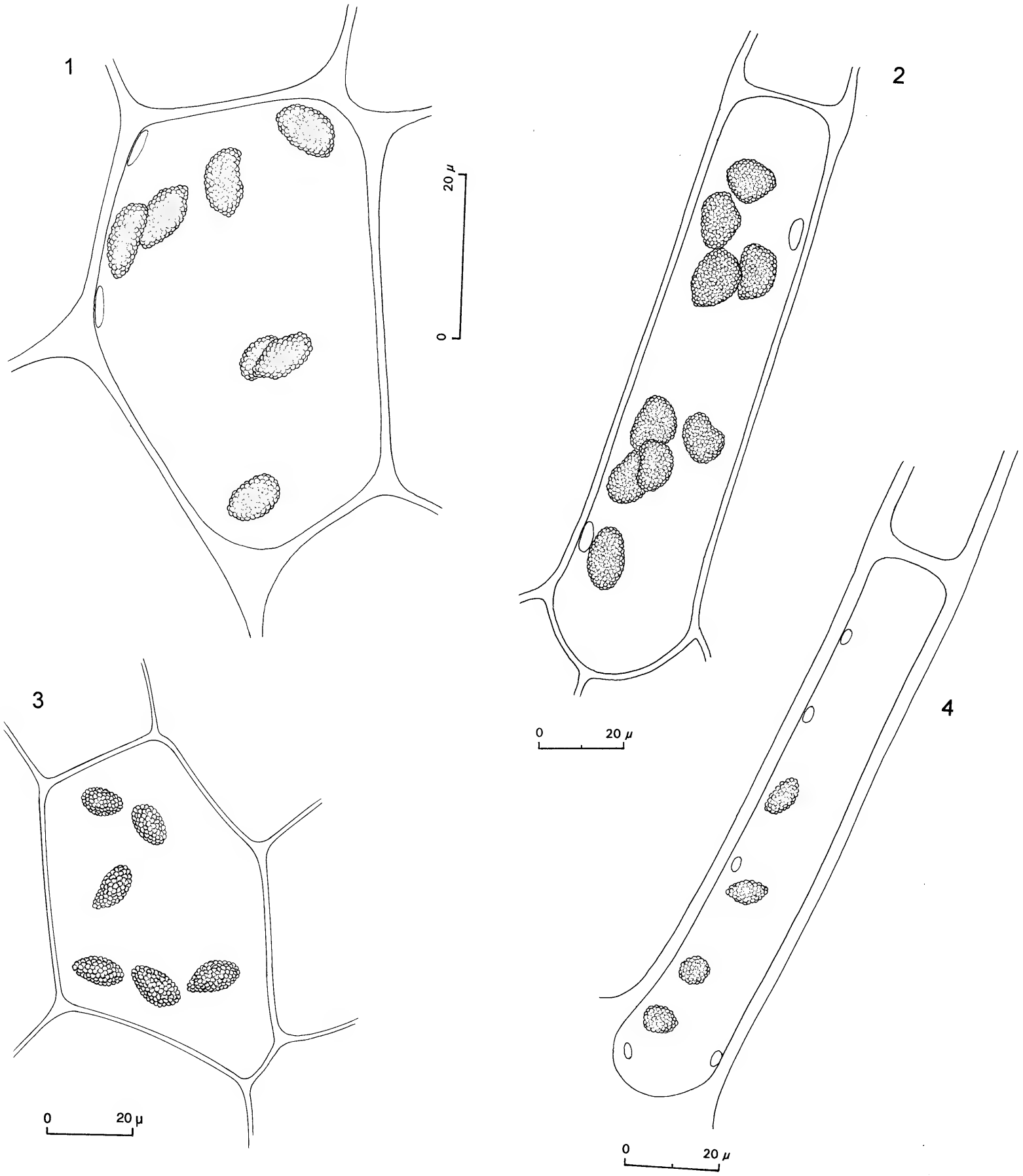

Fig. 77.
Oil-bodies, all (except fig. 3) with the outline of a few chloroplasts included. 1. *Telaranea lindenbergii* (Gottsche) J.J.Engel & Merrill. Disc cell. 2. *Telaranea herzogii* (E.A.Hodgs.) E.A.Hodgs. Basal cell of lobe. 3. *Telaranea martinii* (E.A.Hodgs.) R.M.Schust. Median cell of disc. 4. *Telaranea inaequalis* R.M.Schust. *ex* J.J.Engel & Merrill. Lowermost cell of leaf lobe. (Fig. 1, from *Glenny 9725*, New Zealand, South Is., Westland EP, Tuke R.; 2, from *Glenny 9149*, New Zealand, South Is., Westland EP, Big Wainihinihi R.; 3, from *Engel 24773*, New Zealand, South Is., Westland EP, Cascade Road, just W of Jackson R.; 4, from *Glenny 9352*, New Zealand, South Is., Western Nelson EP, Mt. Augustus.)

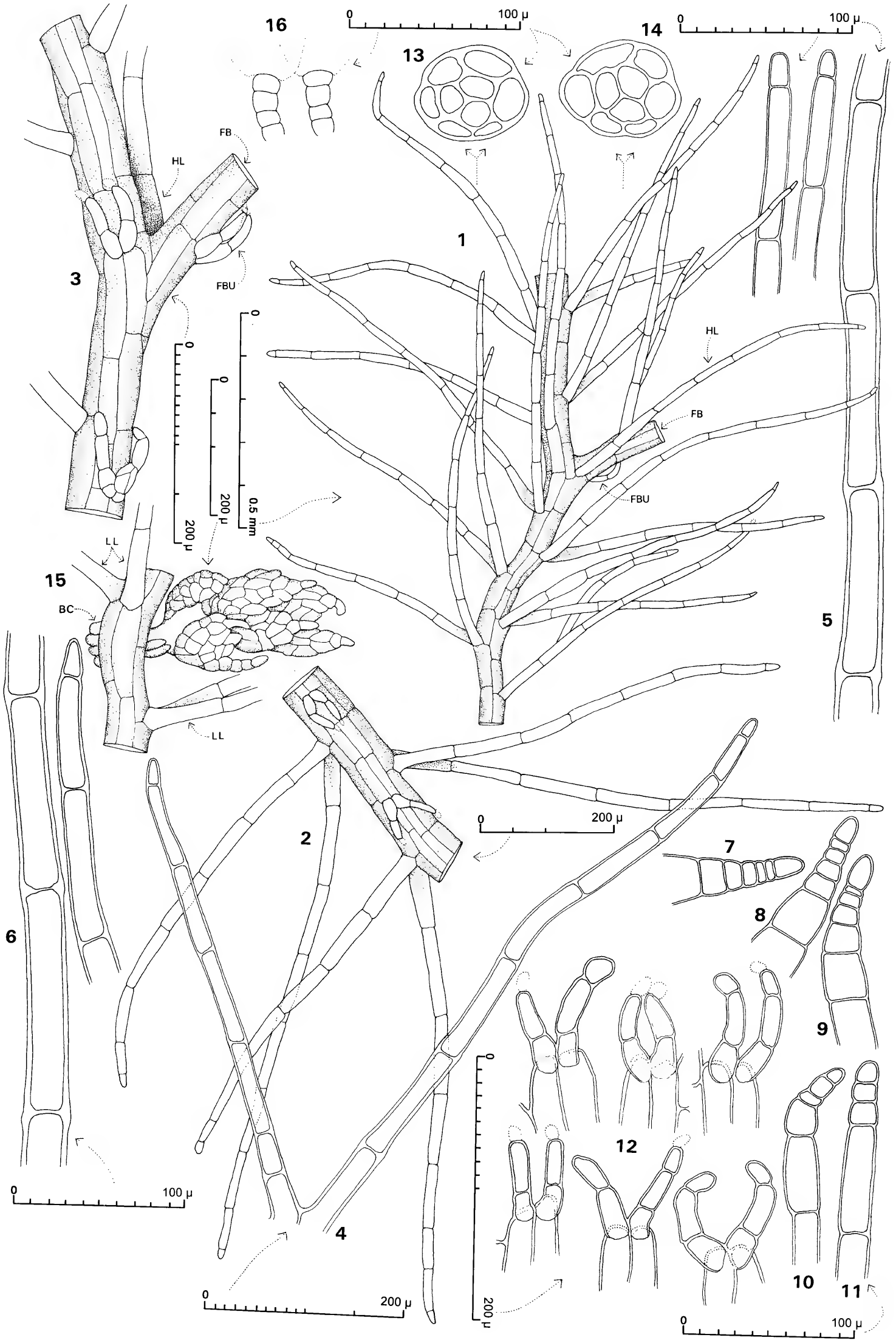

Fig. 78.
Telaranea inaequalis R.M.Schust. *ex* J.J.Engel & Merrill. 1. Dorsal aspect of sector of main shoot with *Frullania*-type branch (= FB; HL = half-leaf; FBU = first branch underleaf). 2. Portion of

Telaranea quinquespina has frequent, leafless, geotropic ventral-intercalary and lateral-intercalary stolons.

"*Telaranea herzogii* var. *nana*" (Schuster, Beih. Nova Hedwigia 118: 230. *f. 77: 4–9*; *79*. 2000, published without a Latin description) is a synonym of *T. herzogii*. The variety was based on a specimen from Stewart Island (*Schuster 60670*).

Telaranea inaequalis R.M.Schust. *ex* J.J.Engel & Merrill

[Fig. 77: 4, oil-bodies, p. 355; Fig. 78]

Telaranea inaequalis R.M.Schust., Beih. Nova Hedwigia 118: 225. *f. 76*. 2000, *nom. nud.* (*sin. descr. lat.*). *Telaranea inaequalis* R.M.Schust. *ex* J.J.Engel & Merrill, Fieldiana, Bot. 44: 117. *f. 37*. 2004. Holotype: Tasmania, Gordon River, Sir John Falls, just upriver from Butler Is., sea level, *Engel 14685B* (F); isotype: (HO).

Plants exceedingly delicate, loosely creeping, the leaf lobes minutely thread-like in appearance, whitish green and nitid; shoots minute, to 1.1 mm wide with leaves. Branching occasional, irregular, of the *Frullania* type; branch half-leaf undivided, leaf-lobe-like; first branch underleaf similar to normal stem underleaves, symmetrically bilobed, the lobes 2–3 cells long, terminating in a slime papilla, inserted on ventral-lateral side of branch just above the base. Flagelliform and stoloniform branches apparently lacking, or rare. Ventral-intercalary branches common, long and leafy. Stems delicate, straight and wiry, rather slender for plant size, the cortical cells in surface view and cross section moderately and evenly thick-walled, in 6 rows (the dorsal larger than the ventral rows); medullary cells in 3(5) rows, smaller, moderately and evenly thick-walled. Main shoots with 2 cortical cells intervening between successive leaves on either side. Rhizoids very thick-walled, from underleaf cells. Leaves distant, widely and laxly spreading, the insertion transverse to at times weakly succubous, consistently bifid essentially to the base (the basal cells scarcely connate), the longer lobes 505–735 μm long, the ventral lobes shorter. Lobes thread-like, not or scarcely tapering, moderately to strongly divergent, flexuous, not disposed in regular ranks, uniseriate throughout, unequal in length: the dorsal (7)8–9 cells long, the ventral 7–8 cells long (not including secondarily divided cells at lobe tips); lobe cells subequal in length except at the tip, the basal cells 22–28 μm wide × 90–120 μm long, the next cell 18–24 μm wide × 78–108(120) μm long, the terminal cell minute, ca. 0.25 the length of the penultimate cell, occasionally with repeated cell divisions at the lobe apex resulting in 3–5 short cells, the tip at times becoming detached; cell walls ± thick-walled, the transverse septa thickened in the corners and feebly swollen and projecting,

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leading shoot, ventral view. 3. Portion of main shoot with *Frullania*-type branch (= FB), ventral view (FBU = first branch underleaf; HL = half-leaf; only the ventral lobes of leaves are shown); note the underleaf at base of figure has 2- and 3-celled lobes and has rhizoid initials formed but rhizoids are lacking. 4. Leaf; note unequal leaf lobes (ventral lobe at left). 5, 6. Leaf lobes (both basal and distal portions included). 7–11. Distal portions of leaf lobes showing subdivision of cells. 12. Underleaves. 13, 14. Stem, cross sections (ventral cortical cells at arrows). 15. Portion of shoot with androecium, oblique-dorsal view (LL = leaf lobe; BC = large cells of collar of the ventral-intercalary androecial branch). 16. Antheridial stalks. (Figs. 1–6, 12–14, from *Engel 14685B*, Tasmania, Gordon R., Sir John Falls; 7–11, 15, 16, from *Jarman 87/5*, Tasmania, Mt. Sprent.)

especially in basal half of lobe, the septa in distal portion of lobe at times weakly constricted; surface smooth. Oil-bodies occupying a very small portion of cell, hyaline and somewhat glistening, (1)2–3(4) per lobe cell, subglobose to elliptic, coarsely papillose, the spherules distinctly protruding. Underleaves small and inconspicuous, bifid, the lobes parallel to somewhat connivent, 2–3 cells long, terminating in a slime papilla, the "disc" formed of the two partially connate lobe cells. Asexual reproduction absent.

Plants dioecious. Androecia on abbreviated, tiny, inconspicuous, ventral-intercalary, spicate branches; bracts closely imbricate, the entire bract deeply concave, bilobed, each lobe terminating in a single cell, or, more often, a uniseriate row of 2 thick-walled cells, the tip cell particularly thick-walled; lamina cells non-tiered, irregular in shape and arrangement, the lamina margins crenulate; antheridia 1 per bract, large for bract size, the stalk uniseriate; bracteolar antheridia absent. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island, South Island (0–900 m); Australia: Tasmania. Known from Rakiura (Pegasus Creek), Fiordland (Bowen Falls) and Western Nelson (Stockton Plateau) EPs.

At Stockton, the species is abundant on sandstone rock overhangs in sharply incised stream valleys, on vertical or overhanging surfaces kept moist by seepage. There it can be the dominant bryophyte, forming dense mats on rock and at the front of overhangs, forming tapering "stalactites" up to 1 m long composed of vascular plant roots (e.g., *Forstera mackayi*), this species, *Acromastigum marginatum* and *A. mooreanum*. Other accompanying species on the rock walls are *Kurzia hippuroides*, *Pallavicinia* aff. *rubristipa*, *Paracromastigum furcifolium*, *Psiloclada clandestina*, *Rhizogonium pennatum*, *Riccardia perspicua*, *Zoopsis bicruris* and *Z. setulosa*.

Comments: *Telaranea inaequalis* is immediately distinct from *T. herzogii* by the consistently unequally bilobed leaves, the flexuous, non-tapering lobes 6–9 cells long (Fig. 78: 4) and the equally and symmetrically bilobed first branch underleaf (Fig. 78: 3). See under *T. herzogii* for additional comments.

Telaranea inaequalis is remarkably similar gametophytically to *T. diacantha* (Mont). J.J.Engel & Merrill of the Neotropics and *T. major* Herzog, a species with a broad distribution ranging from Sri Lanka to the Philippines and Malaysia to Vanuatu. For a discussion see Engel and Merrill (2004).

Kurzia G.Martens

Kurzia G.Martens, Flora 53(27): 417. 1870.
Lepidozia subg. *Microlepidozia* Spruce, J. Bot. 14: 165. 1876. *Microlepidozia* (Spruce) Jörg., Bergens Mus. Skr. 16: 303. 1934.
Dendrolembidium Herzog, Ark. Bot., ser. 2, 1: 497. 1951 (preprint) (1952, journal).
Micrisophylla Fulford, Brittonia 14: 124. 1962.

Plants isophyllous to strongly anisophyllous, ascending to erect, rarely creeping, deep green to olive-green to brown to fuscous, dull-textured, tiny to vigorous. Branching irregularly to regularly 1–2(3)-pinnate, the primary and secondary branches usually ± abbreviated, often weaker, the stems with persistent apical dominance, dendritic in a few species; branches normally all terminal, typically *Frullania* type on one side of axis, *Microlepidozia* type on the

other (the pattern somewhat irregular in some taxa); ventral-intercalary branches present; lateral-intercalary branches present in *Kurzia moniliformis*; main shoots and, more often, lateral branches frequently becoming flagelliform, microphyllous and rhizoid-bearing. Stems firm, the cortical cells in (8)10–20(24) rows, usually thicker-walled and slightly to more often moderately larger than the medullary cells. Leaves usually spreading from stem, the lobes ± erect, the insertion transverse (the leaves then vertically oriented) to ± succubous in a few species (to weakly incubous in *K. helophila*); leaves usually symmetric or virtually so, divided to 0.5–0.75(0.85) their length into 3–4(7) narrow, tapered, subequal to somewhat unequal lobes, the lobe margins usually entire; disc 2–10(12) cells high, the margins with teeth or spurs or entire. Cells small, usually ± firm-walled and rigid, quadrate to oblong but not narrowly rectangular, without trigones; surface mostly papillose to striolate. Oil-bodies small and reduced, or absent. Underleaves from 0.2–0.95 the size of lateral leaves, 3–4(6)-lobed, symmetric or often asymmetric due to abortion of 1–2(3) lobes that terminate in a slime papilla. Asexual reproduction lacking or via caducous leaf lobes.

Dioecious. Androecia usually on abbreviated, ventral-intercalary branches (rarely on leading branches); bracts in 2–8 or more pairs, the antheridia 1 per bract, the stalk 1- or 2-seriate. Gynoecia normally on short ventral-intercalary branches (rarely on long leafy axes), isophyllous, with (2)3–5 series of progressively larger bracts and bracteoles, the innermost with apex 2–4-lobed or -lobulate or crenate-denticulate, the margins often dentate or ciliate. Perianth long, ± fusiform, bluntly trigonous, tapered toward the mouth, the mouth lobulate to ciliate; perianth 2–3(4)-stratose in basal portion.

Seta with 8–10 rows of outer cells surrounding an inner core of 16–18 much smaller cells or (*Kurzia compacta*) 13 rows of outer cells surrounding ca. 42 much smaller cells. Capsule wall 2–3-stratose; outer layer of cells with alternating (secondary) walls with nodular thickenings, the other walls hyaline; innermost layer of cells with semiannular bands complete to incomplete.

Spores papillose to verruculose-vermiculate or with dome-shaped coarse bosses, 1–1.5× diam. of elaters. Elaters bispiral.

Type: *Kurzia crenacanthoidea* G.Martens

A genus of about 32 species. Nine species occur in Australasia, six from our area plus *Kurzia sexfida* (Steph.) Grolle (Tasmania), *K. dendroides* (Carrington & Pearson) Grolle (New South Wales) and *K. verticillata* (Carrington) Grolle (Tasmania). Four species occur in southern South America, all belonging to subg. *Micrisophylla* (Fulford) J.J.Engel *ex* R.M.Schust.; these are *K. setiformis* (De Not.) J.J.Engel & R.M.Schust., *K. mollis* (Steph.) J.J.Engel & R.M.Schust., *K. saddlensis* (Besch. & C.Massal.) Grolle and *K. cucullifolia* (Steph.) R.M.Schust. One species, *K. fragillima* (Herzog) Grolle of Juan Fernandez Islands, was placed in subg. *Microlepidozia* by Schuster (2000a). The genus extends to the Neotropics (three or four species occur there according to Gradstein et al., 2001) and four are cold-Laurasian. The genus ranges through the Paleotropics north to Japan. The phylogenetic analysis in Engel and Merrill (2004) indicated that *Kurzia*, as defined by the presence of *Microlepidozia*-type branching, is polyphyletic, and five species previously assigned to *Kurzia* were transferred to *Telaranea*. The transferred species from our area are *K. quadriseta*, *K. trilobata*, *K. fragilifolia* and *K. quinquespina*.

Until relatively recently, the name *Microlepidozia* (Spruce) Jörg. was used for this genus,

until Grolle (1964b, 1965e) resurrected the older generic name *Kurzia* G.Martens, which was originally applied to a minute species believed to belong to the red algae (*Rhodophyta*). *Kurzia* contains five subgenera; subg. *Microlepidozia* and subg. *Dendrolembidium* occur in New Zealand.

As Engel and Merrill (2004) demonstrated, *Kurzia*, as traditionally constituted, is polyphyletic. The circumscription of *Kurzia* is more uniform after the transfer to *Telaranea* of several taxa (Engel and Merrill, 2004). *Kurzia* is characterized by a number of features, some occurring throughout the genus, others distinct tendencies; these are: 1) presence of *Microlepidozia*-type branching; 2) underleaf lobes differentiated; 3) plants often developing brownish or fuscous pigmentation; 4) leaves and underleaves with a dense areolation, comprised of evenly thick-walled cells that are small in size and always devoid of trigones; 5) leaves and underleaves often armed with spurs or teeth; 6) surface of leaf lobes and disc typically striate-papillose; 7) leaves usually transversely oriented, and often deeply and palmately (3)4-lobed, with narrow, linear to lanceolate lobes; 8) plants, even when helophytic, tend to have a relatively firm cortex, normally somewhat to strongly thick-walled; 9) leafy shoots tending to develop geotropic, microphyllous axes and lateral leafy branches infrequently or not tapered and rhizoidous; and 10) oil-bodies small and reduced or absent.

References: Engel and Merrill (1996b); Engel (2005a); Grolle (1964b); Hodgson (1956); Schuster (1969c, 1980a, 2000a).

Key to Species

1a. Plants not strikingly dendroid, lacking a sharp separation into phototropic, initially unbranched, erect axes that are freely and closely 2–3-pinnate distally and geotropic, fasciculate, root-like stolons; leaves lacking basiscopically directed, numerous finger-like appendiculi of disc base. Subg. *Microlepidozia* 2

2a. Disc margins of leaves and half-leaves consistently entire; leaf surface smooth; cortical cells 5–9 intervening between successive leaves on each side of stem. Sect. *Helophilae* . . . . . *K. helophila* (p. 362)

2b. Disc margins of some or all leaves toothed or spurred; leaf surface papillose; cortical cells 2–5 intervening between successive leaves on each side of stem 3

3a. Leaf lobes submoniliform, the lobe cells short, barrel-shaped, distinctly constricted at the septa; leaves commonly fragmenting (lobes sometimes missing but disc usually intact); lateral-intercalary branches present; perianth surface scabrous (prorate) in distal sector. Sect. *Moniliformes* . . . . . *K. moniliformis* (p. 373)

3b. Leaf lobes straight-sided, the lobe cells not or at most feebly constricted at the septa; leaves not fragmenting; lateral-intercalary branches absent; perianth surface smooth 4

4a. Disc margins on each side with 1(5) spinose teeth; sinus bases lacking spines or reflexed armature; leafy shoots erect, originating as ventral-intercalary branches from a leafless, reddish brown stolon, the erect shoots usually compactly pinnately branched. Leaf lobes (4)5–7 cells wide at base. Sect. *Compactae* . . . . . *K. compacta* (p. 377)

4b. Disc margins on each side with a single tooth, or with a basal abaxial spur near the margin (if unarmed, then disc of half-leaf with 1 or more teeth);

sinus bases often with spines; leafy shoots both horizontal and erect, the ascending to erect shoots arising as terminal branches from a horizontal leafy axis (which becomes denuded with age). Leaf lobes 2–4 cells wide at base (to 7 cells wide in *K. calcarata*). Sect. *Microlepidozia* 5

5a. Disc and lobes densely areolate, the cells 12–18(20) μm wide, subquadrate, evenly thick-walled; disc margins armed on either side with short, stout, thorn-like teeth (rarely absent, but then half-leaves have teeth); leaves small (250–400 μm wide), stiff and rigid, the disc widely spreading to squarrose, the lobes spreading, or more typically suberect and parallel with the stem; sinus bases and abaxial face of disc unarmed, or (var. *ornata*) with irregular, broad-based laminar outgrowths. Leaf lobes 2–4 cells wide at base (4–6 cells wide in var. *ornata*) . . . . . *K. hippuroides* (p. 368)

5b. Disc and lobes laxly areolate, the cells 20–27 μm wide, rather thin-walled; disc margins armed on either side near the base with a spreading, often decurved spur; leaves larger (500–750 μm wide), cupped, suberect from a laxly spreading disc, the lobes gently incurved; sinus bases and abaxial face of disc with 1–several slender, fleshy appendages, when well developed forming a basiscopic fringe or comb extending across the face of the disc (at times rudimentary or lacking in some or all leaves). Leaf lobes (2)4–7(8) cells wide at base . . . . . *K. calcarata* (p. 364)

1b. Plants strongly dendroid: with a sharp division into erect, initially unbranched axes that distally form a closely 2–3× pinnately branched "frond," and creeping rhizomes from which arise geotropic, branched, fasciculate, root-like flagella; leaves with a conspicuous comb of basiscopically directed, tapered, finger-like processes arising from the base of the high disc; underleaves large, 4–6-lobed, similarly basally armed. Subg. *Dendrolembidium* . . . . . *K. tenax* (p. 379)

Subg. ***Microlepidozia*** (Spruce) R.M.Schust.

Lepidozia subg. *Microlepidozia* Spruce, J. Bot. 14: 165. 1876. *Microlepidozia* (Spruce) Jörg., Bergens Mus. Skr. 16, 303. 1934. *Kurzia* subg. *Microlepidozia* (Spruce) R.M.Schust., J. Hattori Bot. Lab. 48: 355. 1980. Type: *Microlepidozia pauciflora* (Dicks.) Schljakov, Novosti Sist. Nizsh. Rast. 13: 226. 1976.

Sect. ***Helophilae*** R.M.Schust.

Kurzia sect. *Helophilae* R.M.Schust., Beih. Nova Hedwigia 118: 259. 2000. Type: *Kurzia helophila* R.M.Schust.

Kurzia helophila R.M.Schust.

[Plate 6E]

Plants anisophyllous, stiff and wire-like, erect or suberect, densely caespitose, turf-forming, golden brown to dark brownish or fuscous (new growth often greenish), freely branched, the shoots to 5 mm wide, including branches. Branching mostly terminal (*Frullania* and *Microlepidozia* type), distantly and sympodially branched (rarely 1- or 2-pinnate), the branches dorsally ascending, typically overtopping as new leading shoots, not becoming microphyllous; branch half-leaf linear, 2-lobed to 0.4–0.6; first underleaf of *Frullania*-type branch 3–4-lobed, inserted on ventral-lateral side of branch base and aligned with underleaves of branch; branch leaves 3–4-lobed. Ventral-intercalary branches rather common, stoloniform, or ascending and giving rise to new shoots. Stem epidermal cells in 10–12(16) rows, weakly to moderately thick-walled (surface view), brownish, larger than the leptodermous or weakly incrassate, usually hyaline medullary cells; cortical cells 5–9 intervening between successive leaves on each side of stem. Leaves distant to crowded on the same shoot, hand-like, often distinctly cupped, the disc obliquely spreading, the lobes incurved, the insertion transverse to weakly incubous; leaves (180)300–400(420) μm long and wide, variable in shape, symmetric to somewhat asymmetric, longer than broad, ± equally (3)4(5)-lobed to 0.5–0.6 (median sinus), often bisbifid and then lobes in pairs. Lobes attenuate, (3)4–8 cells broad at base, entire, ending in a single cell or a uniseriate row of 2–3 cells. Disc symmetric to weakly asymmetric, (5)7–10(12) cells high at median sinus, unarmed, the margins entire. Cells of leaf disc with walls brownish, moderately and evenly thickened, the cells ca. 16–18 × 17–24 μm; lobe cells quadrate, ± isodiametric; surface smooth. Underleaves ca. 0.4–0.5 the area of leaves, concave, symmetric or asymmetric, 4-lobed to 0.45–0.8 (typically 1–2[3] lobes somewhat shorter, ending in slime papillae), sometimes weakly bisbifid, the normal lobes attenuate; disc 5 cells high at median sinus; disc margins entire. Asexual reproduction absent.

Androecia rather elongated, normally determinate, compactly spicate, on ventral-intercalary or terminal-lateral branches, the ♂ branch rarely with limited proliferation vegetatively distally (the androecium then basal on a rather short branch); bracts in 4–7 pairs, ventricose-cucullate, 2–3-lobed to ca. 0.3, the lobes acute, at times apiculate, the dorsal margin sparingly crenate, the bract cells leptodermous; antheridia 1 per bract, the stalk biseriate. Gynoecia (only young known) on short to weakly elongated ventral-intercalary branches; bracts shallowly lobed at summit, the lobes sharp to blunt, entire to weakly few-dentate. Perianth (immature) shallowly lobulate at mouth, the lobes 2–6 cells broad at base, drawn out into acuminate apices usually formed of 1–2 strongly elongated cells (4–7:1), the perianth at base 3–4-stratose, becoming unistratose distally and formed of narrow, elongated cells.

Sporophyte not seen.

Comments: *Kurzia helophila* differs from all other New Zealand species of the genus in the smooth surface, the tall disc (typically 7–9 or even 10–11 cells high) and the complete absence of armature on both leaf and underleaf margins. The leaves are lax, concave and frequently bisbifid, the median sinus noticeably deeper than the others. Plants of *K. helophila* are usually sparingly branched, the branches often overtopping the main shoot. The color of the plants is fuscous to a clear brown and may be used to distinguish the species when growing together with other *Kurzia* species. The leaves are very variable in shape, but there is never any indication of teeth of disc or of lobes.

The species tends to grow erect, with ascending branches. At least some phenotypes regularly produce what can only be described as slender roots: the main axis, usually 105–115 μm wide and with cell walls fuscous and thickened, gives rise to very slender, ventral-intercalary geotropic axes that are pale brown or colorless and often only 32–45 μm in diam. These have narrowly rectangular, relatively thin-walled cortical cells. We have not seen such striking dimorphism between rather rigid stems (and ascending branches) and slender, flagelliform axes in any other *Kurzia* species; their microphyllous branches are never as slender. The erect main axes, mostly 10–15 mm high, may bear "roots" some 4–6 mm long from lower sections of main axes, and such roots appear never to ramify. The leafy shoot is pinnulate with leafy branches that often taper distally and become small-leaved; such branch apices never become nearly as slender as the "roots."

Other extremes (e.g., the type of var. *flaccida*) seem to wholly lack the slender geotropic microphyllous axes.

The two varieties of the species may be distinguished as follows:

Key to Varieties

1a. Leaves 0.5–0.65 quadrifid or bisbifid; disc (5)7–9 cells high; cells of basal portions of leaf lamina considerably larger than in upper parts and in lobe bases; main axis with cortical cells in 10–12 rows . . . . . var. *helophila* (p. 363)

1b. Leaves 0.4–0.55 quadrifid; disc 9–11(12) cells high; cells of leaf lamina subequal in size from base into basal halves of lobes; main axis with cortical cells to 16 rows . . . . . var. *flaccida* (p. 364)

Kurzia helophila R.M.Schust. var. ***helophila***

Kurzia helophila R.M.Schust., J. Hattori Bot. Lab. 48: 368. *f. 6: 1–16*. 1980. Type: New Zealand, South Is., Westland Prov., near Omoeroa River, N of town of Fox Glacier, *Schuster 67-236*.

Main axis with cortical cells in (10)12 rows; leaves quadrifid or bisbifid to 0.5–0.65; disc (5)7–9 cells high; cells of basal portions of leaf lamina considerably larger than in upper parts and in lobe bases.

Distribution and Ecology: Endemic to New Zealand: South Island (320–1370 m), North Island (920–1320 m). Known from Fiordland, Southland, Otago, Westland, Western Nelson, Southern North Island (Tararua Ra.) and Taranaki EPs.

Kurzia helophila, as the name suggests, is always helophytic. It occurs over a rather broad altitudinal range. Like *K. calcarata*, it may occur in open, sunny, moory, low-lying coastal areas, highly acidic, either where low *Halocarpus biformis*, *Leptospermum scoparium* and *Phyllocladus alpinus* dwarfed trees grow, admixed with *Empodisma minus*, or in open pakihi, growing mostly under *Gleichenia*, adjacent to or mixed with other *K. calcarata*, *Riccardia* spp., *Lethocolea pansa* and *Neogrollea notabilis*. The species also occurs at higher elevations (550–1370 m), but is confined to boggy, exposed ground, in *Oreobolus pectinatus*, *Donatia novae-zelandiae*, *Phyllachne colensoi* cushion bog, with *O. impar*, *Drosera arcturi*, *D. spathulata* and *Lycopodiella diffusa*, at times mixed with *Sphagnum cristatum* and *S. falcatulum*. At Sewell Peak (Paparoa Ra., 890 m), for example, it occurred in penalpine

Chionochloa, *Dracophyllum longifolium*, *Celmisia* and *Empodisma minus* on the ground among cushion plants. At the summit area of Te Rangaakapua (Urewera Natl. Park, 1265–1320 m) it occurs in open, saturated, mucky depressions in a mosaic of stunted *Olearia colensoi* and tussock with occasional *Coprosma* spp. At this site, plants at times grow very tightly compact, with only the shoot tips at the surface level. Accompanying species are *Calliergonella cuspidatum*, *Campylopus acuminatus* var. *kirkii*, *Cephaloziella nothogena*, *Cephalomitrium aterrimum*, *Cheilolejeunea novae-zelandiae*, *Drepanocladus aduncus*, *Hygrolembidium acrocladum*, *Riccardia aequitexta*, *R. crassa* and the lichen *Siphula decumbens*.

Kurzia helophila var. ***flaccida*** R.M.Schust. *ex* J.J.Engel

Kurzia helophila var. *flaccida* R.M.Schust., Beih. Nova Hedwigia 118: 259. 2000, *nom. nud.* *Kurzia helophila* var. *flaccida* R.M.Schust. *ex* J.J.Engel, Novon 17: 310. 2007. Holotype: New Zealand, South Is., Fiordland Natl. Park, track from L. Mackenzie to Harris Saddle, *Schuster 67-3908* (F).

Plants fuscous, main shoots ca. 525–550 μm broad, with cortical cells in (12)15–16 rows. Leaves somewhat incubously inserted, hand-like, strongly concave, tending to be clearly longer than broad, ovate to obovate, ca. 275–330 μm wide × 350–415 μm long, infrequently bisbifid, divided to 0.55; disc 17–24 cells broad, 9–12 cells high. Underleaves variable, often asymmetrically 4-lobed, some to only 0.4–0.5.

Distribution and Ecology: Endemic to New Zealand. Known only from the type, which occurred in alpine tussock grassland, in peaty areas among *Sphagnum*, *Metahygrobiella drucei* and *Hygrolembidium* between 1100 and 1250 m.

Comments: This extreme tends to have a higher disc, often as high or higher than broad. The leaf lamina is formed of almost equal-sized cells throughout the lamina and well into the lobes. By contrast, in var. *helophila*, the basal cells in the lamina are considerably larger than those of the upper portions of the disc and of the basal halves of the lobes.

This plant is closely similar in many respects to the southern South American *Kurzia saddlensis*. Vigorous shoots may be subisophyllous. However, on other shoot sectors underleaves may be relatively small and abnormal; deeply bisbifid underleaves sporadically occur. It is possible that this is merely a luxuriant extreme of "normal" *K. helophila*.

Sect. ***Microlepidozia***

Kurzia calcarata (Steph.) Grolle

Plants lax, erect or suberect, loosely interwoven to caespitose, clear brown, the shoot apices pale green, the shoots medium, to 8 mm wide, including branches. Branching rather freely 1(2)-pinnate, the erect leafy branches terminal (of both *Frullania* and *Microlepidozia* types), the branches dorsally ascending, the branching frequently subopposite; shoots sporadically flagelliform; branch half-leaf 2-lobed to 0.8, the disc margins with a spinose tooth; first underleaf of *Frullania*-type branch 4-lobed, inserted on the ventral-lateral side of base of branch and aligned with underleaves of branch. Ventral-intercalary branches occasional, leafy and devel-

oping into new leading shoots, or leafless, geotropic and stoloniform. Stems distinctly flexuous; cortical cells short-rectangular, slightly thick-walled, the walls brownish, feebly striolate in surface view, in ca. 12 rows, surrounding a leptodermous medulla of ca. 24–28, moderately smaller cells; cortical cells 2–4 intervening between successive leaves on each side of stem. Leaves soft, lax, cupped, distant to imbricate, the lobes gradually incurved, ca. 400–500 × 500–750 μm, wider than long, the insertion transverse; leaves often highly variable on the same plant, symmetric, ± equally 4-fid to ca. 0.6–0.7(0.85) on strongest shoots, to ca. 0.5 on branches as well as sectors of main shoot. Lobes variable, often somewhat curved, long-attenuate, entire or with 1–several marginal teeth, ± contracted at the base, (2)4–7(8) cells broad, tapered to a uniseriate row of (2)3–4 cells; cells of the uniseriate row isodiametric to ± elongated (to 2.5:1), the terminal cell tapering to a blunt tip. Disc symmetrical, (2)4–6 cells high to as much as 8(10) cells high in shallowly lobed leaves (both extremes at times on same shoot); disc armature highly variable (sporadically developed or lacking in some or all leaves), the sinus bases and the abaxial face of disc typically with one or more acuminate, multicellular fleshy appendages, 1–several cells wide at base, at times forming a basiscopic fringe or "comb" extending across the base of the disc or only in vicinity of the margin, or the armature confined to 1–2 spurs arising near sinus base; one or both margins armed near the base with a strong, often falcate, spur-like tooth. Cells of lobe bases relatively large, with moderately thin, brownish walls, mostly 20–27 × 20–36(40) μm; surface delicately to distinctly and coarsely papillose. Oil-bodies (Schuster, 2000a) 1–3 in most or almost all leaf cells, small for cell size, formed of a few coarse segments. Underleaves subequal to leaves in size or a little smaller, subsymmetrically (3)4-fid to ca. 0.6, with abaxial armature absent, or disc surface sporadically armed as in leaves; disc 3–5 cells high, the margins armed as in leaves. Asexual reproduction absent.

Androecia spicate, on ± short to long indeterminate ventral-intercalary branches, the branches either initially produce vegetative leaves followed by ♂ bracts or, more often, initially produce androecia and proliferate vegetatively distally, the androecia respectively either intercalary or basal on a branch; bracts ventricose-cucullate, strongly dorsally assurgent, the base obliquely spreading, the lobes erect, the bracts bilobed to ca. 0.4 by narrowly acute to acuminate segments; dorsal and ventral margins of disc similar, each with a tooth near segment base, the dorsal completely smooth or with a few slime papillae near base; antheridia 1 per bract, the stalk uniseriate; bracteolar antheridia lacking. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the branches often initially with several cycles of microphyllous leaves; bracts of innermost series much larger than leaves, erect and closely ensheathing the perianth, the bracts concave, narrowly ovate to elliptic, shallowly 2–4-lobed, the lobes composed of thin-walled rectangular to subrhomboidal cells, the apical end of the marginal cells often diverging and forming a crenulation or tooth, the lobes terminating in a single cell or a uniseriate row of 2 rather elongate cells; lamina composed of ± regularly short- to long-rectangular, leptodermous cells, the margin sparingly and irregularly dentate-ciliate; bracteole similar in size and form. Perianth very large for plant size, straight to curved, long-fusiform, terete below, the distal sector pluriplicate and gradually narrowing to the contracted mouth, the mouth splitting into several narrowly attenuate divisions each sparingly crenulate by the projecting distal end of a marginal cell, the divisions terminating in a single cell or 2 laterally juxtaposed, rather thick-walled, somewhat elongated cells that are laterally free for varying lengths; perianth unistratose throughout.

Sporophyte not seen.

Comments: *Kurzia calcarata* is distinguished from *K. hippuroides* in several important respects. The stem cortical cells are relatively thin-walled and the leaf cells are noticeably larger

(20 μm or more wide) and appear thinner walled than those of *K. hippuroides*, even under the dissecting microscope. The leaf cell walls are a rich, clear brown and the surface more faintly and distantly papillose.

Leaf armature in *Kurzia calcarata* is variable. Expressions with extreme development of armature from the sinus bases and the abaxial face of the disc were described by Schuster (1980a) as a distinct species, *K. temnomoides*; however, the same degree of ornamentation is found in the type of *Lepidozia calcarata* (G!). There is a continuum within the species, ranging from phenotypes with almost unarmed leaves to those with occasional abaxial spurs, to those with prominent, basiscopically reflexed spurs, arising at or below the sinus bases, forming a "comb," reminiscent of *K.* (*Dendrolembidium*) *tenax* (p. 379). In the latter, however, the abaxial transverse comb is more strongly developed and typically arises at or near the leaf base, rather than at or just below the sinus base; *K. tenax* is also a much larger plant, with elaborate, dendritic branching, lacking in *K. calcarata*.

Leaves of *Kurzia calcarata* also vary with respect to lobe width and depth of lobing, from strongly cupped, shallowly divided leaves, with the disc to 8(10) cells high, to deeply divided leaves with a low disc (2–4 cells high) and slender, narrow lobes, 2–3(4) cells wide. The leaves of the type of *K. calcarata* are 5–7(8) cells high, with lobes (4)5–7(8) cells wide.

Two phases may be distinguished, as follows:

Key to phases

1a. Leaves deeply divided, to 0.6–0.7(0.85), the disc (2)4–7(8) cells high; lobes lanceolate, often abruptly contracted at base; normally with abaxial spur-like processes; branching pinnate from a prostrate runner . . . . . *K. calcarata s. str.* (p. 366)

1b. Leaves shallowly divided, to 0.5 or less, the disc to 8–10 cells high; lobes shorter and broader, not or little contracted at the base; disc only rarely with abaxial processes (but with marginal armature); plants caespitose, branching not regularly pinnate, the branches overtopping . . . . . "concava" phase (p. 367)

Kurzia calcarata (Steph.) Grolle (typical phase)

Lepidozia calcarata Steph., Sp. Hepat. 3: 592. 1909. *Microlepidozia calcarata* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 257. 1963. *Kurzia calcarata* (Steph.) Grolle, Rev. Bryol. Lichénol. 32: 178. 1964 (1963). Lectotype (*fide* Engel and Merrill, 1996b): New Zealand, without specific locality, 27 Dec. 1885, *Kirk 1887*, ex herb. Kew (G!).

Kurzia temnomoides R.M.Schust., J. Hattori Bot. Lab. 48: 371. *f. 7*. 1980, *syn. fide* Engel and Merrill, 1996b. Type: New Zealand, South Is., Westland Prov., N of Omoeroa River, S of town of Franz Josef, *Schuster 67-251*.

Leaves deeply divided, to 0.6–0.7(0.85), the disc (2)4–7(8) cells high; lobes lanceolate, often abruptly contracted at base; disc usually with abaxial spur-like processes; branching pinnate from a prostrate runner.

Distribution and Ecology: New Zealand: South Island (50–1420 m), North Island (65–1500 m), Chatham Islands (250 m); Australia: Tasmania (Schuster, 1980a, p. 373), Queensland. In New Zealand known from Fiordland, Southland, Otago, Westland, Western Nelson, Southern North Island (Ruahine and Tararua ranges), Volcanic Plateau, Auckland and Northland EPs.

A helophytic species, growing in full sunlight, over a rather broad altitudinal range. It occurs over waterlogged acidic peaty soil with impeded drainage (pakihi), as well as in boggy areas to 1280 m, at times forming dense tufts among *Sphagnum* hummocks. For example, it occurs in open *Sphagnum – Empodisma minus – Halocarpus biformis – Phyllocladus alpinus* moor-like sites (Westland). The type of *Kurzia temnomoides* was collected in a *Sphagnum – Empodisma minus – Halocarpus – Phyllocladus alpinus* bog, exposed to the direct sun. At the upper end of its altitudinal range (e.g., at Rainbow Skifield in the St. Arnaud Ra., 1360–1480 m; Mt. Robert Skifield, W end of Lake Rotoiti, 1400–1480 m), plants occur, for example, in mosaics of tussock grass and alpine vegetation along with tarns, rills, rocky outcrops and boulderfields, and in such sites they occur in rills draining the tarns (where it may form large pure masses), at the edges of tarns, at times submerged and at times among *Sphagnum*. It also occurs under prostrate mats of dead tussock blades, a niche that was notably warmer to the touch at midday. In Urewera Natl. Park, Waikareiti Track, Waipai Swamp (720 m), it occurred at the edge of a *Sphagnum* mat in a low, open, boggy area with *Sphagnum* hummocks, *Leptospermum scoparium* and *Dracophyllum subulatum*. South of Te Whakapatiki on the Herangi Ra. (S of Kawhia Harbor, ca. 720–750 m) plants occurred on an exposed plateau that includes a cushion bog (dominated by *Oreobolus pectinatus* and with common associates *Cyathodes empetrifolia*, *Lepidothamnus laxifolius* and *Baumea tenax*) that is surrounded by rocky outcrops, low shrubland (<2 m) in which *Leptospermum scoparium*, *Quintinia serrata* and *Dracophyllum traversii* are prominent, with *Sphagnum* as ground cover in wetter sites and small trees (<6 m) including *Weinmannia*. At this site *K. calcarata* occurred on moist soil with *Sphagnum* beneath 1 m scrub adjacent to the bog. On the Hauraki Plain and on Chatham Island it is found in *Sporodanthus* bog. It has been found with *Campylopus clavatus*, *C. introflexus*, *Eotrichocolea polyacantha*, *Hygrolembidium rigidum*, *Lepidozia obtusiloba*, *Megaceros giganteus*, *Pseudocephalozia lepidozioides* and *Telaranea herzogii*.

Kurzia calcarata (Steph.) Grolle ("concava" phase)

Plants erect, caespitose. Leaves (and underleaves) cupped, or even hemispherical, with strongly incurved lobes; disc to 10 cells high, typically with a lateral spur on each side, arising from the upper part of disc or lower sector of lobe (reduced to lacking in some leaves); abaxial spurs not or rarely present.

Distribution and Ecology: Endemic and known at present from only two localities in Otago: Swampy Summit, northwest of Dunedin (*Child H1924*, F), and Ajax Hill, Catlins River area (*Child H5508*, F), at elevations of 455–610 m. The plant occurs in open boggy ground, with *Sphagnum cristatum*, *Riccardia cochleata*, *Riccardia* sp., *Kurzia tenax* and *Verdoornia succulenta*, and at the Ajax Hill locality, with *K. helophila*.

Comments: This expression resembles *Kurzia helophila* in the caespitose habit and irregular branching, the branches erect and overtopping the main axis, as well as in the concave, shallowly divided leaves with attenuate, incurved lobes. The typical phase differs in the abaxially armed leaves, with more long-tapered, lanceolate leaf lobes. In the "concava" phase the lobes end in a single cell, scarcely elongated (or in 2 cells side-by-side) vs. in a uniseriate row of (2)3–4 cells in the typical phase. In the "concava" phase the leaves, examined dorsally, appear slightly incubously inserted and the leaves somewhat postically deflexed vs. leaves transversely inserted and oriented in the typical phase.

Kurzia hippuroides (Hook.f. & Taylor) Grolle
[Plate 6F; Figs. 79, 80]

Plants slender and wiry, variable in pigmentation from pale green to yellowish green to deep brown, in loosely interwoven mats (less commonly erect and caespitose), the shoots small to medium, to 6 mm wide, the main shoot at times becoming flagelliform, microphyllous, whip-like and brownish. Branching basically 1–2(3)-pinnate, in well-developed plants with erect, pinnate terminal branches (both *Frullania* and *Microlepidozia* types), produced at ± regular intervals from a horizontal, indeterminate, leafy axis that becomes denuded with age (shoots mostly erect in compact, caespitose expressions), the branching frequently subopposite, the branches dorsally ascending, the ultimate ones sometimes dorsiventrally flattened, with leaf lobes dorsally assurgent; erect leafy branches sporadically becoming flagelliform and whip-like; branch half-leaf deeply 2-lobed to 0.8 (or divided to the base into two halves), the margins with a spinose tooth; first underleaf of *Frullania*-type branch 2–3-lobed, inserted on the ventral-lateral side of base of branch and aligned with underleaves of branch. Ventral-intercalary branches from the horizontal axis erect and leafy, or leafless, glistening, geotropic and stoloniferous, often long and whip-like (to 2.5 mm or more long). Stems stiff and wiry; cortical cells elongate, distinctly thick-walled (especially the radial longitudinal walls), the walls greenish to (often) brown; 2–4 cortical cells intervening between successive leaves on each side of stem. Leaves brittle, rigid, ± concave to canaliculate, distant on the main axis to densely imbricate on the ultimate branches, the disc widely spreading to squarrose, the lobes widely spreading or becoming ± abruptly suberect and parallel with stem (the stem leaves suberect and appressed), ca. 200–250 × 250–400 μm, the insertion transverse; leaves symmetric, ± equally 4-fid to ca. 0.6–0.75 (median sinus). Lobes narrowly attenuate, at times sublinear and ± straight-sided, plane or ± contracted and ventrally sulcate at base, consisting of regular tiers of small quadrate or short-oblong cells; lobe margins entire or sporadically with 1(2) marginal teeth, terminating in a single cell or a uniseriate row of 2–3(4) cells, the cells of uniseriate row ± elongate (2:1) on stem leaves to subquadrate on leaves of ultimate branches; lobes 2–4(6) cells wide at widest point. Disc 2–4 to (var. *ornata*) 4–6 cells high; sinus bases and abaxial face of the disc variously appendaged, the lobe margins and abaxial face of disc with laminar outgrowths or vertical lamellae (in var. *ornata*), or the disc armature sporadically developed, rudimentary or lacking; disc margins each with a single tooth (when unarmed in most leaves, the branch half-leaf consistently toothed); branch leaves typically with disc margins entire. Cells of disc and lobes evenly thick-walled, subquadrate to short-rectangular, small, often only ca. 12–18(20) × 14–22 μm; base of disc with a distinct abaxial row of enlarged supporting cells; surface of disc and lobes finely to distinctly papillose. Underleaves usually asymmetrically 4-fid to near the base, the lobes slender, 2–3 cells wide at the base (1–2 lobes often reduced and uniseriate for most of their length); disc 1–2 cells high, unarmed or rarely with a marginal tooth. Asexual reproduction absent.

Androecia on short, determinate, ± spicate, ventral-intercalary branches from leading shoots (in both leafy and flagelliform sectors); bracts ventricose-cucullate, bilobed to ca. 0.3 by acuminate segments that terminate in a uniseriate row of 2–3 cells; dorsal and ventral margins of disc similar, sparingly denticulate-dentate, the dorsal with a few slime papillae, otherwise smooth; antheridia 1 per bract, large for bract size, the stalk uniseriate; bracteolar antheridia lacking. Gynoecia on abbreviated ventral-intercalary branches issuing from older sectors of main stem and from stoloniform branches, the gynoecium base swollen and rhizoidous; bracts of innermost series much larger than leaves, erect and closely ensheathing the

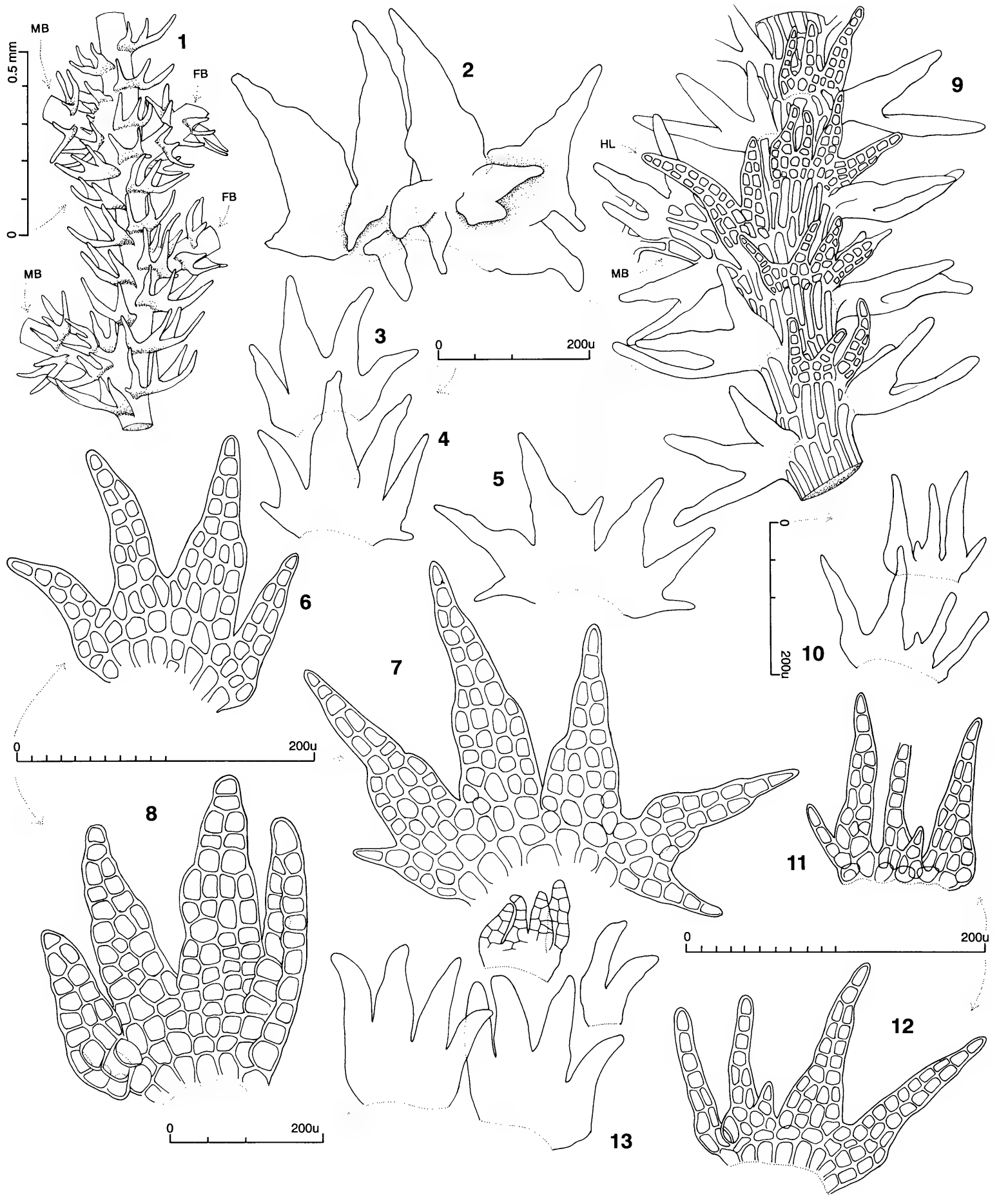

Fig. 79.
Kurzia hippuroides (Hook.f. & Taylor) Grolle (figs. 1, 3–13, var. *hippuroides*; 2, var. *ornata* (Steph.) J.J.Engel & Merrill). 1. Sector of main shoot, dorsal view; *Frullania*-type branches (= FB) at right and *Microlepidozia*-type branch (= MB) at left, dorsal view. 2–5. Leaves. 6–8. Leaves, cellular detail. 9. Sector of main axis, ventral view, with *Microlepidozia*-type branch (= MB) and half-leaf (= HL). 10. Underleaves. 11, 12. Underleaves, cellular detail. 13. Two leaves and (above) an underleaf (lobes with cellular detail), and a half-leaf. (Figs. 1, 3, 6, 9, from type of *K. hippuroides*; 2, from type of var. *ornata*; 4, 5, 7, 10–12, from *Engel 18690*, New Zealand, South Is., Fiordland EP, Borland Road; 8, 13, from type of *K. allisonii*.)

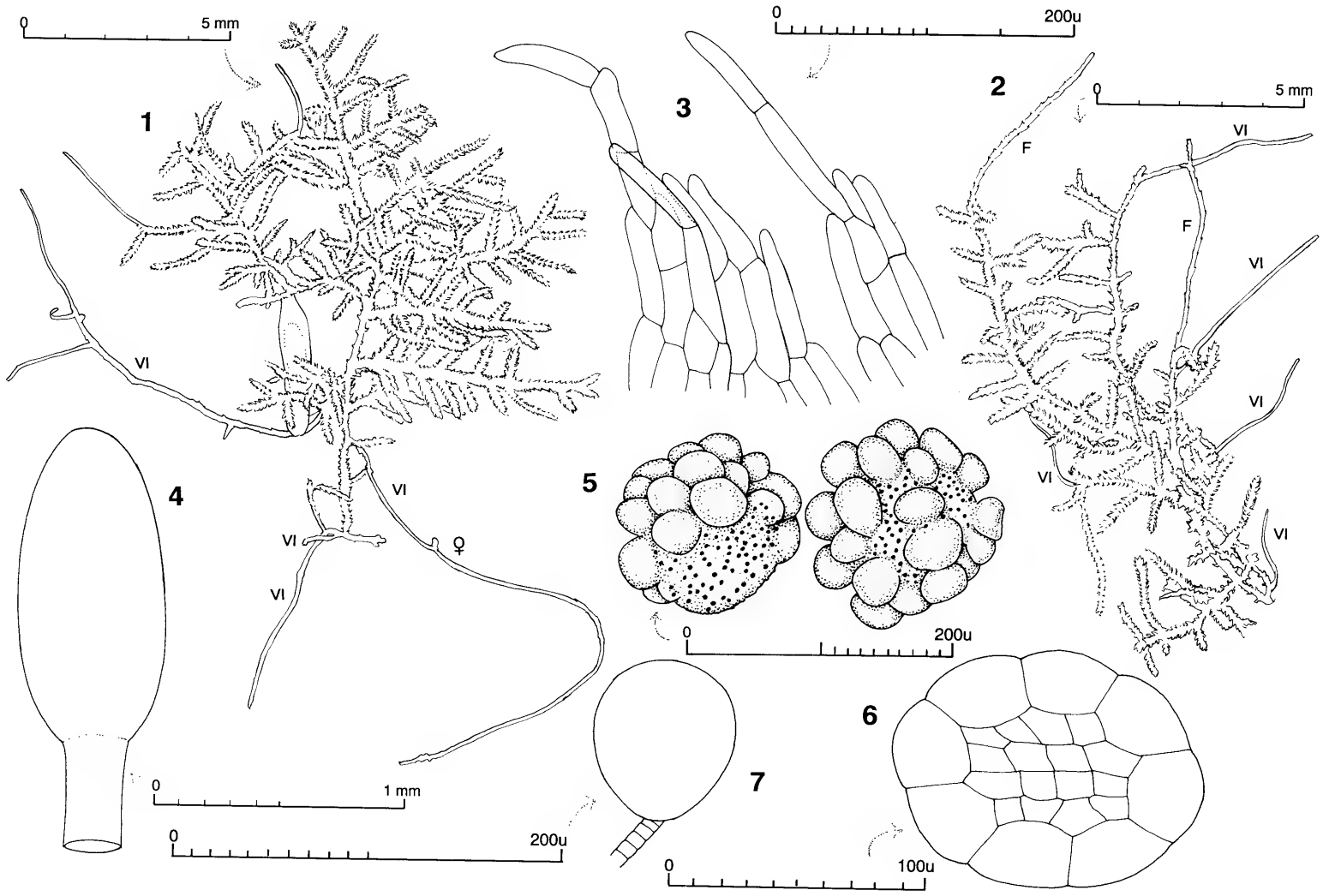

Fig. 80.
Kurzia hippuroides (Hook.f. & Taylor) Grolle. 1, 2. Plants, all branches terminal unless otherwise indicated (F = *Frullania*-type branch; VI = ventral-intercalary branch; ♀ = juvenile gynoecium); note that leading shoots may become flagelliform and that perianth (in fig. 1) originates from leafless stolon. 3. Portions of perianth mouth. 4. Capsule profile. 5. Spores, proximal face shown at left. 6. Seta, cross section. 7. Antheridium. (Figs. 1, 2, 4–6, from *Engel 19001*, New Zealand, South Is., Westland EP, track to Alex Knob; 3, from *Engel 17727*, New Zealand, South Is., Otago EP, summit of Mt. Maungatua; 7, from *Engel 19293*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., Croesus Track.)

perianth, the bracts membranous, concave, narrowly ovate to subrectangular to obovate, shallowly 2–4-lobed, the lobes markedly leptodermous, broad at base, the summit blunt and dentate-subciliate by elongate cells that are partially or wholly laterally free and rounded at the tip; lamina composed of ± regularly short- to long-rectangular to 5–6-angled, leptodermous cells, the margin irregularly and sparingly crenate-dentate, especially distally; bracteole similar in size and form. Perianth very large for plant size, straight to curved, fusiform, terete and often ± stipitate below, the distal sector clearly 3-plicate and ± gradually narrowing to the contracted, ± contorted mouth, the mouth fringed with cilia and unicellular teeth that are partially or completely laterally free, the cilia terminating in a uniseriate row of up to 4 cells, the armature cells thin-walled, elongate; perianth bistratose in basal sector.

Seta with 8 rows of outer cells surrounding an inner core of 16 much smaller cells. Capsule rather long-ellipsoidal, the wall 29–36 μm thick, of 2–3 layers; outer layer of cells ± regularly narrowly rectangular, with two-phase development, the longitudinal walls with thin, sheet-like thickenings and sparing nodule-like to occasionally spine-like thickenings alternating with walls that are devoid of thickenings, the transverse walls devoid of thickenings; innermost

layer of cells ± tiered, irregularly narrowly rectangular cells, semiannular bands common, narrow, close and numerous, usually complete, rarely forked.

Spores 12–13.9 μm in diam., brown, with dome-shaped, coarse bosses (to 3.4 μm in diam.) that are sometimes irregular (through coalescence of adjacent bosses) and with the intervening spore wall papillose. Elaters rigid, nontortuous, 10.6–12.5 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.4–4.8 μm wide.

Comments: *Kurzia hippuroides* is interpreted broadly in the sense of Engel and Merrill (1996b) to include all New Zealand representatives of the genus with rigid, deeply lobed, squarrose-spreading leaves; small (10–18 μm wide), evenly thick-walled, subquadrate leaf cells; and variable development of disc armature and ornamentation. Pigmentation ranges from light green to dark brown. The cortical cells of the stem are elongate, narrow and distinctly thick-walled.

Optimally developed populations typically have prostrate, leafy "runners," with erect, closely pinnate "fronds" (Fig. 80: 1, 2). The resulting habit is reminiscent of a miniature "running-pine" (*Lycopodium complanatum*). In compact, densely caespitose forms the interconnection between erect, leafy shoots is often obscured.

Grolle (1964b, p. 178) describes *Kurzia hippuroides* as "sehr formenreich," but two marked expressions may be recognized within the species:

Key to Varieties

1a. Leaf disc 2–3 cells high; lobes attenuate, 2–4 cells wide at base, plane; sinus and disc armature sporadically developed or lacking, the disc margins often entire, sinus teeth rarely present . . . . . var. *hippuroides* (p. 371)

1b. Leaf disc 4–6 cells high; lobes acute, 4–6 cells wide at widest point, contracted and ± ventrally sulcate at base; sinus bases dilated and reflexed, the lobe margins and abaxial face of the disc variously elaborated with basiscopic spines or vertical lamellae . . . . . var. *ornata* (p. 373)

Kurzia hippuroides var. ***hippuroides***

Jungermannia hippuroides Hook.f. & Taylor, London J. Bot. 3: 387. 1844 ("*hippurioides*"). *Lepidozia hippuroides* (Hook.f. & Taylor) Steph., Sp. Hepat. 3: 594. 1909. *Microlepidozia hippuroides* (Hook.f. & Taylor) E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. *Kurzia hippuroides* (Hook.f. & Taylor) Grolle, Rev. Bryol. Lichénol. 32: 178. 1964 (1963). Type: Auckland Is., Nov. 1840, *Hooker* (FH!).

Jungermannia dispar Mont. *ex* Taylor & Hook.f. *in* Hook.f., Bot. Antarc. Voy. 1: 158. (ante May) 1845. *Jungermannia dispar* Mont. *ex* Hook.f. & Taylor, London J. Bot. 3: 388. 1844, *nom. nud.* *Lepidozia dispar* (Mont. *ex* Taylor & Hook.f.) Mont. *in* Dumont d'Urville, Voy. Pôle Sud, Bot. 1: 248 (Aug.) 1845; Ann. Sci. Nat., Bot. III, 4: 353. (Dec.) 1845. *Mastigophora dispar* (Mont. *ex* Taylor & Hook.f.) Trevis., Cat. Herb. Crypt. 2: 30. 1853. *Telaranea dispar* (Mont. *ex* Taylor & Hook.f.) E.A.Hodgs., Rec. Domin. Mus. 4: 107. 1962. Lectotype (*fide* Engel and Merrill, 1996b): Auckland Is., *Hombron*, ex herb. Montagne (FH!).

Lepidozia allisonii Herzog, Trans. Roy. Soc. New Zealand 68: 43. *pl. 5, f. a–c*. 1938. *Microlepidozia allisonii* (Herzog) R.M.Schust., J. Hattori Bot. Lab. 26: 257. 1963. *Kurzia allisonii*

(Herzog) Grolle, Rev. Bryol. Lichénol. 32: 178. 1964 (1963). Holotype: New Zealand, North Is., 12 miles E of Taupo, 2 Dec. 1933, *Allison 227* (JE! – *c. per.*); isotype: (MPN, *non vidi*).

Armature of leaf disc and sinuses sporadically developed or lacking, the disc margins often entire, sinus teeth rarely present; leaves with disc 2–3 cells high, the lobes attenuate, 2–4 cells wide at base, plane.

Distribution and Ecology: New Zealand: Auckland Islands, Campbell Island, Stewart Island (5–690 m), South Island (2–1250 m), North Island (160–1280 m), Chatham Islands; Australia: Tasmania, Victoria. In New Zealand known from Fiordland, Southland, Otago, Westland, Western Nelson, Southern North Island (Tararua Ra., Hawkes Bay), Volcanic Plateau (Tongariro Natl. Park, Atiamuri), Gisborne, Auckland and Northland EPs.

More mesophytic and shade tolerant than our other species in subg. *Microlepidozia*. It occurs in forests of all types (*Nothofagus*, tall podocarps, *Weinmannia*) from near sea level to upper elevations (to over 850 m), over inorganic substrates such as the soil of the forest floor or mossy banks, or on organic substrates such as decaying, bryophyte-covered logs and stumps, soil in caves formed by tree roots, as well as tree-fern bases (particularly the dead stumps) and occasionally on the trunks themselves. When under forest it is found with *Bazzania adnexa*, *B. nitida*, *Fissidens pallidus*, *Leucobryum candidum*, *Mittenia plumula*, *Rhizogonium distichum*, *R. pennatum*, *Zoopsidella caledonica*, *Zoopsis argentea* and *Z. leitgebiana*.

Kurzia hippuroides extends into the penalpine zone in areas of *Chionochloa*, *Dracophyllum longifolium*, *Olearia colensoi*, *Celmisia* and *Empodisma minus*, occurring on the ground, at times forming damp swards between tussocks. The species also occurs in pakihi and in *Carex* swamps. In such open sites it occurs with *Campylopus bicolor*, *C. clavatus*, *Pulchrinodus inflatus* and *Riccardia crassa*.

Kurzia hippuroides is the most drought-tolerant species of the genus. It may occur, for example, on exposed soil of paths on steep slopes as far north as Radar Bush (WSW of Cape Reinga) and here, despite the rigorous habitat, forms perianths. Phases growing in forests, in partial or deep shade, on soil or humus, often in disturbed areas, as along paths, may be bright yellowish green. At the opposite extreme, helophytic phases (which may occur with *K. tenax*, *K. calcarata* and *K. helophila*, as on Swampy Summit, Otago) may be deeply infuscated and show a considerably different growth pattern.

On Stewart Island occurring loosely on ground of litter and soil under dense *Gleichenia* at 5 m in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium* – *Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus* (track to Mason Bay, Freshwater Landing). Also at the Mt. Rakeahua summit area (600–690 m) over exposed soil between boulders in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* from 0.5 m to 2 m tall and significant areas of exposed rock.

Comments: The type of *Jungermannia hippuroides* consists of plants that are rather small and compact, and the leaves have a low disc with weakly developed armature (Fig. 79: 3, 6, 9). The type of *Lepidozia allisonii* also consists of small plants, but not so minute as the original description (Herzog, 1938) would suggest. In addition, the disc margins, particularly on the more vigorous shoots, are frequently toothed (not entire as described), the disc is frequently more than 2 cells high and the leaf lobes are often broader than 2 cells wide (Fig. 79: 8).

The form and arrangement of terminal branches are distinctive. They are frequently subopposite, dorsally ascending and with leaf lobes dorsally assurgent. The ultimate branches are

sometimes strongly dorsiventrally flattened as in *Hatcher 298* (Waipoua Forest), whereas the type of *Kurzia hippuroides* has somewhat complanate branches, but not to the same degree.

Kurzia hippuroides var. ***ornata*** J.J.Engel & Merrill
[Fig. 79: 2]

Kurzia hippuroides var. *ornata* J.J.Engel & Merrill, J. Hattori Bot. Lab. 80: 228. 1996. Holotype: New Zealand, South Is., Southland Prov., Mt. Burns, ca. 5000 ft., *Child H3351* (F).

Leaf disc 4–6 cells high; lobes acute, 4–6 cells wide at widest point, contracted and ± ventrally sulcate at base; sinus bases dilated and reflexed, the lobe margins and abaxial face of the disc variously elaborated with basiscopic spines or vertical lamellae.

Distribution and Ecology: Endemic to New Zealand: South Island (25–1525 m), North Island (1265–1320 m).

The var. *ornata* occurs in scattered stations, for the most part in forests of *Nothofagus menziesii* or of *N. solandri* var. *cliffortioides* above 500 m and may be found on soil over shaded, vertical cliff faces, at times forming very loose, felt-like mats lining the pockets of the cliff faces. Also in the alpine zone; for example, on the plateau and slopes below Mt. Burns (Fiordland) it occurred over soil under grass overhang of a steep slope (1225–1320 m). Known from one station in the North Island: under rather thick layer of tussock blades at 1265–1320 m in a mosaic of stunted *Olearia colensoi* and tussock with occasional *Coprosma* spp. (Urewera Natl. Park, Huiarau Ra., summit area of Te Rangaakapua). The type (Mt. Burns) occurred as a damp sward between tussocks at 1525 m.

Comments: The reflexed sinus bases and laminar outgrowths of the lobes and abaxial face of the disc (Fig. 79: 2) distinguish this expression. In addition, the lobes are broader than those of the typical form and ± contracted at the base. The armature of the leaves is somewhat reminiscent of that in *Lepidozia ornata* (compare Fig. 79: 2 with Fig. 35: 2, 3 of *L. ornata*).

Sect. ***Moniliformes*** J.J.Engel

Kurzia sect. *Moniliformes* J.J.Engel, Cryptogamie 26: 77. 2005. Type: *Kurzia moniliformis* J.J.Engel.

Kurzia moniliformis J.J.Engel
[Fig. 81]

Kurzia moniliformis J.J.Engel, Cryptogamie 26: 73. *f. 1*. 2005. Holotype: New Zealand, North Is., South Auckland Prov., Kaimai-Mamaku Forest Park, Kaimai Ra., spur ESE of Ngatamahinerua, headwaters of Poupou Stream, ca. 2 km W of North-South Track, 405 m, *Engel and von Konrat 23600* (F); isotype: (AK).

Plants with a prickly appearance, wiry, pure green to pale olive-green, the stems golden brown, forming interwoven, compact, felt-like mats, the shoots tiny for genus, to 3 mm wide including branches, the main shoot often becoming flagelliform, pale, microphyllous and

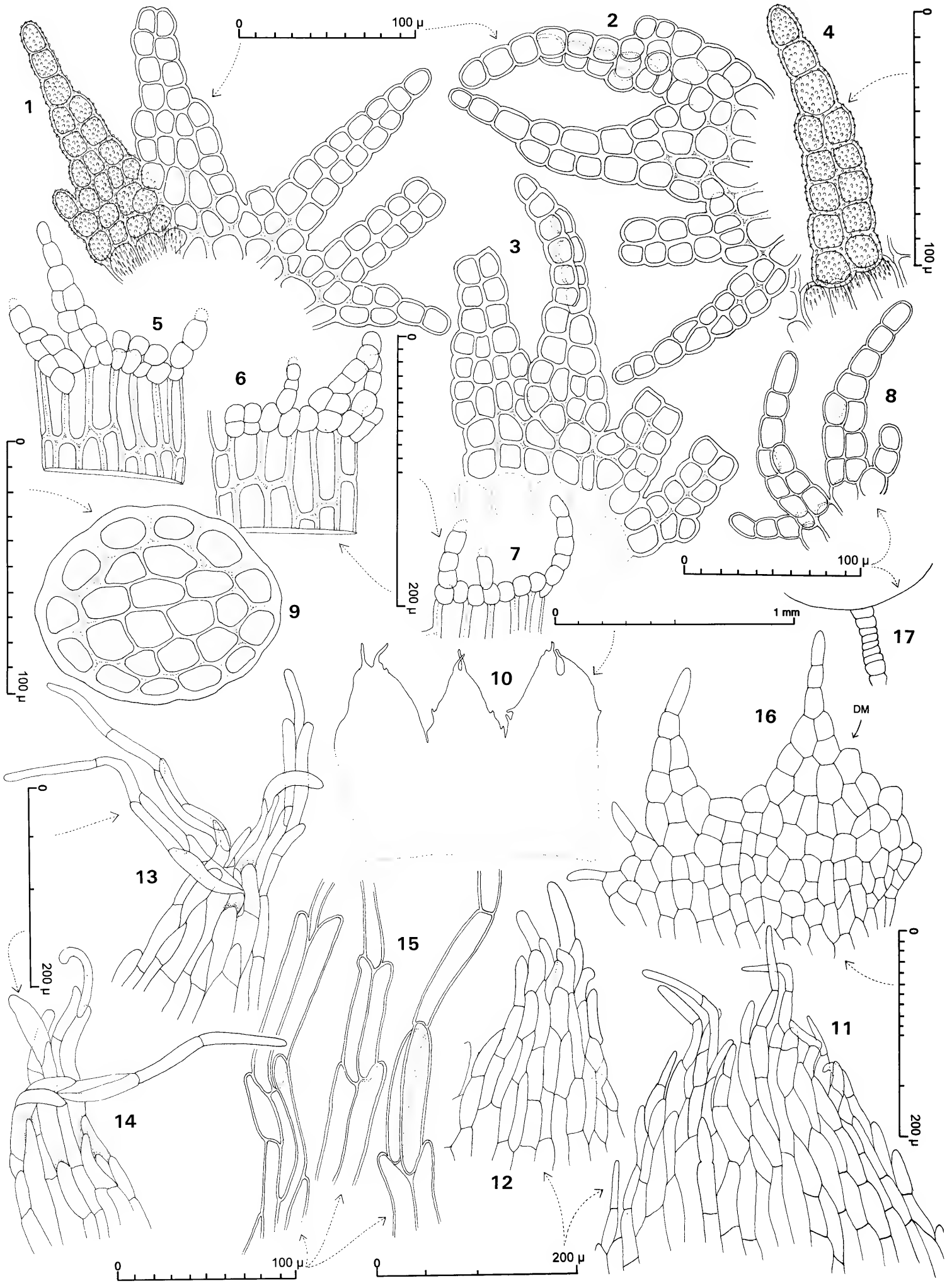

Fig. 81.
Kurzia moniliformis J.J.Engel. 1–3. Leaves of main axis, the surface detail shown in part at left in fig. 1; stipple at base of fig. 3 indicates stem cells (all drawn to same scale). 4. Lobe of leaf from main axis, adaxial view (note papillose surface, but basal half of disc cells is smooth). 5–7. Underleaves of main shoot (all drawn to same scale). 8. Half-leaf. 9. Stem of prostrate main shoot, cross section. 10. ♀ Bracts and bracteole; note fusion of basal half. 11. Portion of apex of ♀ bract.

appearing similar to stolons. Branching basically 1–2(3)-pinnate, with suberect, pinnate terminal branches (both *Frullania* and *Microlepidozia* types), produced at ± regular intervals from a horizontal, indeterminate, leafy axis that becomes denuded with age, the branching frequently subopposite, the branches dorsally ascending and at right angles to the main shoot, the ultimate ones somewhat dorsiventrally flattened, the erect leafy branches not becoming flagelliform; branch half-leaf divided to the base into two halves, each half variously inserted in relation to the other, each similar to a leaf lobe, the margins each with a lateral spur, or entire; first underleaf of *Frullania*-type branch asymmetrically or (sporadically) symmetrically 3-lobed, inserted on the ventral lateral side of base of branch. Ventral-intercalary branches from the horizontal axis, becoming erect and leafy, or geotropic and stoloniform, often long and whip-like. Lateral-intercalary branches occasional, from flagelliform sectors in distal portion of plant, the branches pinnate and similar to those that are terminal in origin. Stems stiff and wiry, the cortical cells in surface view elongate, distinctly thick-walled (especially the radial longitudinal walls), the walls golden brown, the cortical cells in cross section in 12 rows, in a single layer of very thick-walled, pigmented cells slightly larger than the firm-walled, colorless, medullary cells; 3–4 cortical cells intervening between successive leaves on each side of stem. Rhizoids sparsely developed, from cells of underleaf disc. Leaves brittle, rigid, firmly attached, concave to canaliculate, distant on prostrate leading axes, but rather densely imbricate on ultimate branches, the disc widely spreading to squarrose, the lobes ± abruptly suberect and parallel with stem, or with lobe tips arched toward the stem, the dorsal-most lobes somewhat more stiffly erect on leaves of the main shoot but markedly so on the branches, the branch leaves appearing as if "brushed" forward; leaves 120–145 μm wide × 125–170 μm long, the insertion transverse, the leaves somewhat asymmetric due to differing size and form of lobes, ± equally 4-fid nearly to the base. Lobes easily fragmenting, with varying portions of the lobes at times caducous, the leaves sometimes lacking the entire lobe, at times just the uniseriate sector, the lobes narrowly attenuate to narrow-sublinear, 2–4 cells broad at base and with up to 6 biseriate tiers and in that sector hardly tapering, terminating in a uniseriate row of 2–3 cells that are distinctly constricted at the septa, the lobe margins entire; lobe cells comprised of small, quadrate to short-oblong cells, turgid and barrel-shaped lending the uniseriate portion a submoniliform appearance, the cells of uniseriate row subisodiametric to at most slightly elongated (to ca. 1.3:1), the terminal cell rounded at the tip. Disc 1(2) cells high; sinus bases and abaxial face of the disc without appendages; disc often with a single tooth on dorsal margin, the ventral margin entire or sporadically with a small tooth; disc of primary branch leaves sporadically with a tooth on dorsal margin, the leaves of the ultimate branches typically with disc margins entire. Cells of disc and lobes evenly rather thick-walled and without trigones, subquadrate to short-oblong, small, those in basal half of lobe 10–17 × 16–22 μm, those of disc 15–18 × 12–20(24) μm; surface of lobes distinctly papillose on both abaxial and adaxial faces, the papillae crowded, the surface of disc striate. Underleaves usually asymmetrically (3)4-fid to near the base, the lobes 2 cells wide at the base followed by 0–3 biseriate tiers and a uniseriate row of 2–5 cells, the cells of uniseriate row mostly similar in appearance to those of leaves; fully developed lobes typically more persistent, with a uniseriate row of up to 5 subisodiametric cells and with a terminal cell lacking a slime papilla; aborted lobes weaker in appearance, thinner-walled, often readily caducous, consisting of (1)2 cells that are

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12. Lobe of ♀ bract. 13, 14. Portions of perianth mouth; note articulated cilia and prorate cells below. 15. Basal portion of 3 cilia of perianth mouth showing articulated cells. 16. ♂ Bract (DM = dorsal margin). 17. Antheridial stalk. (All from type.)

either subisodiametric or at times 2:1 or a little more, the terminal cell often with a slime papilla; disc 1–2 cells high, the cells subisodiametric, thick-walled, the margins entire; underleaves of older shoot sectors often consisting solely of the disc + paired cells of lobe bases. Asexual reproduction via fragmenting leaves.

Androecia on short, determinate, spicate, ventral-intercalary branches from leading leafy shoots, on both ventral- and lateral-intercalary branches in flagelliform sectors; bracts up to 6 pairs, strongly ventricose-cucullate, leptodermous throughout, bilobed to ca. 0.4 by acuminate segments that terminate in a uniseriate row of 2–3 cells; dorsal and ventral margins of disc similar, the ventral with 1–2, few-celled teeth, the dorsal with smaller, delicate cells in basal sector, often with a tooth just below level of lobe; antheridia 1 per bract, large for bract size, the stalk uniseriate; bracteolar antheridia lacking. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the gynoecium base swollen and densely rhizoidous; bracts and bracteole of first series small and scale-like, those of second series tightly appressed to those of innermost series; bracts and bracteole of innermost series erect and closely ensheathing the perianth, identical, markedly membranous, fused and tubular in basal half, the free portion of bracts and bracteole each concave, shallowly bilobed, the lobules broad at base, terminating in an elongate process composed of 1–2 elongate, papillose cells, the lobule margin crenate-denticulate by projecting distal ends of cells; free sector of lamina composed of ± regularly short- to long-rectangular to 5-angled cells, the margin irregularly crenate-dentate. Perianth straight to curved, fusiform, terete in basal half, stipitate at the base, the distal half obscurely trigonous and pluriplicate, narrowing to a distinct, rather elongate contracted sector at the mouth, the mouth fringed with cilia, the cilia composed of 1–2 biseriate tiers of elongate cells each free distally and forming a shoulder-like projection and terminating in a single, thin-walled, elongate cell or a uniseriate row of 2 such cells (to ca. 7:1), the perianth surface directly below scabrous by free distal ends of cells (prorate).

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand. Known only from the type, which occurred in the Kaimai Ra. under the shade of a *Blechnum* colony in a stream valley under an open canopy of *Beilschmiedia tawa* and *Weinmannia silvicola*; the subcanopy dominants were *Schefflera digitata*, *Cyathea dealbata* and *C. smithii* and a shrub layer of *Freycinetia baueriana* and *Cortaderia*.

Comments: This is a distinctive species that should not be confused with any other New Zealand member of the genus. Leaf lobes are distinctive in having up to 6 biseriate tiers and in that sector hardly taper (Fig. 81: 1, 4). Lobes terminate in a uniseriate row of 2–3 cells that are turgid, barrel-shaped and distinctly constricted at the septa, which lends the uniseriate portion submoniliform (Fig. 81: 1–4). The lobe cells below the level of the uniseriate row also notably bulge (Fig. 81: 1, 3). The leaves are comprised of small, quadrate to short-oblong cells that do not much differ from leaf apex to base (Fig. 81: 1–3). Cells are evenly thick-walled, and the surface of the entire leaf is distinctly papillose except for the striate disc (Fig. 81: 1, 4). For further comments see Engel (2005a).

Sect. ***Compactae*** R.M.Schust.

Kurzia sect. *Compactae* R.M.Schust., J. Hattori Bot. Lab. 48: 381. 1980. Type: *Kurzia compacta* (Steph.) Grolle.

Kurzia compacta (Steph.) Grolle

[Fig. 85: 1, oil-bodies, p. 394]

Lepidozia compacta Steph., Sp. Hepat. 3: 592. 1909. *Microlepidozia compacta* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 257. 1963. *Kurzia compacta* (Steph.) Grolle, Rev. Bryol. Lichénol. 32: 178. 1964 (1963). Type: New Zealand, *Lauterbach*.

Plants clearly anisophyllous, vigorous, rigid, erect and becoming semidendroid, green to olive-green to reddish brown toward the base, shoots to 1.5 cm wide, including branches. Branching of the short, erect, leafy, green shoots somewhat irregularly to regularly and compactly 1–2-pinnate (*Frullania* and *Microlepidozia* types), the branches dorsally ascending, the erect shoots typically originating as ventral-intercalary branches from a leafless (or microphyllous) reddish brown stolon, both stolons and erect leafy shoots also bearing brownish, geotropic, microphyllous stolons; branch half-leaf 2-lobed to ca. 0.75, the lobes occasionally sparingly toothed, the disc margins on each side with 1–2 spinose teeth or a lobuliform process; first underleaf of *Frullania*-type branch (2)3-lobed, inserted on ventral-lateral side of branch base and aligned with underleaves of branch; branch leaves 4-lobed. Ventral-intercalary branches rather common (the leafy shoots being primarily intercalary in origin), leafy or stoloniform. Stems with cortical cells thick-walled but large and pellucid, in ca. 12 rows, larger than the hyaline, leptodermous medullary cells; cortical cells 4–5 intervening between successive leaves on each side of stem. Leaves markedly rigid, moderately concave, approximate to imbricate, ca. 300 × 350–450 μm, the lobes gradually becoming suberect from a spreading disc, the insertion transverse; leaves symmetric, broader than long, equally 4-lobed to ca. 0.65. Lobes slenderly and evenly attenuate, entire or with 1–2 spinose marginal teeth, the median lobes (4)5–7 cells wide at base, the lateral lobes 4–5 cells wide at base, terminating in a uniseriate row of 2–3 cells; cells of uniseriate row typically broader than the cells beneath, often elongate, the terminal cell tapering to a point. Disc (3)4–5(6) cells high, one or both margins with 1(2–5) spinose, erect to spreading teeth, the teeth commonly 2–3 cells long; spines in sinus bases lacking (rarely with marginal teeth at base of lobes); abaxial face of disc without accessory armature. Cells of disc-middle evenly thick-walled, quadrate to subrectangular, ca. 12–20 × 19–26 μm, typically with a row of larger, elongated cells along the insertion on the abaxial leaf face; lobe cells ± isodiametric, often in regular tiers; surface of disc striate-papillose (rarely almost smooth), the lobes densely and often coarsely papillose. Oil-bodies inconspicuous, obscure, occupying a small fraction of cell, hyaline, mostly 1, sporadically 2 or 3 in basal part of lobe, fusiform to crescentic, coarsely papillose, only slightly larger than chloroplasts. Underleaves large, 0.45–0.6× the leaf area, asymmetrically 4-fid, with 2(3) lobes few-celled and often uniseriate for most of their length or aborted, ending in a slime papilla, the remaining lobes approaching those of the leaves in size and shape. Asexual reproduction absent.

Androecia not seen. Gynoecia on abbreviated ventral-intercalary branches issuing from basal, leafless sectors of main stem, the gynoecium base swollen and rhizoidous; bracts much larger than leaves, all erect and closely ensheathing the perianth, those of innermost series membranous, deeply concave-canaliculate, narrowly ovate; apices 4-dentate-lobulate, the armature leptodermous, each tooth or lobule consisting of a single cell or 2–3 laterally juxtaposed cells that are variously laterally free, or a short, acute process terminating in a uniseriate row of 2 cells, the apex otherwise crenulate; lamina composed of ± regularly short- to long-rectangular, leptodermous cells, the margin bordered by cells variable in shape and orientation, most long and narrow and with the apical or free end variously divergent and form-

ing a short projection or a tooth, the margin irregularly crenulate to crenate-denticulate, occasionally with a ciliiform process; bracteole similar in size and form. Perianth very large for plant size, straight to slightly curved, fusiform, terete below, at times obscurely trigonous in median sector, the distal sector clearly pluriplicate and gradually narrowing to the contracted mouth, the mouth fringed with ca. 10 narrowly attenuate, laciniiform processes that usually terminate in a uniseriate row of 2, elongate, thin-walled cells or sporadically in a single elongate cell, the mouth appearing fringed with cilia; perianth bistratose in basal sector.

Seta with 13 rows of outer cells surrounding an inner core of ca. 42 much smaller cells. Capsule ellipsoidal-cylindrical in immature state.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5–530 m), South Island (10–900 m), North Island (5–1320 m). Known from Fiordland, Southland, Otago, Westland, Western Nelson, Southern North Island, Volcanic Plateau, Auckland and Northland EPs.

The species, frequent in the South Island, occurs on inorganic substrates over a rather broad altitudinal range, like several other New Zealand members of the genus. It occurs on soil in pakihi bogs and extends to upper elevations in open, boggy or damp sites. In the Paparoa Ra., for example, it is a penalpine plant on the sides of rills in an area of *Celmisia*, *Chionochloa rubra*, *Dracophyllum longifolium* and *Empodisma minus* (immediately N of Sewell Peak, 890 m). In such areas it may form swards under snow tussock, or, exceptionally, may even occur deep in rock crevices or on soil over rock. It also may occur in protected pockets of alpine fellfields (Tongariro Natl. Park, headwaters of Mangawhero River, 1630 m). At the summit area of Te Rangaakapua (Urewera Natl. Park, 1265–1320 m) it is rather common in a mosaic of stunted *Olearia colensoi* and tussock with occasional *Coprosma* spp., and at this site it occurs on soil of the floor or of vertical small banks. Of interest is the presence of this species in the central North Island frost flats, a habitat subject to desiccation and one that is wholly marginal for Hepaticae, consisting of an open, low area with scattered *Leptospermum scoparium*, *Dracophyllum subulatum* and abundant *Cladonia* (near Otupaka Stream, 13 km SW of Minginui).

On Stewart Island it was found deep in a protected pocket of a rock crevice in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma* (Mt. Rocky summit area, 530 m). Also near sea level on Stewart Island, and at Port Pegasus the species occurred on a vertical rock face immediately below Belltopper Falls in an open, humid niche dominated by bedrock with a forest margin of *Weinmannia racemosa* and *Dracophyllum*.

Comments: The loosely organized branching pattern of mature, well-developed plants of this species is fundamentally different from that of *Kurzia calcarata* in that the erect green leafy shoots arise as intercalary innovations from horizontal, leafless (or microphyllous) reddish brown stolons, as well as occasionally from other erect leafy shoots. Brownish, geotropic, microphyllous stolons normally originate from basal, leafless sectors of upright shoots, or from other stolons. The system of prostrate stolons and intercalary, erect leafy shoots is found in several other *Lepidoziaceae*, such as *Pseudocephalozia paludicola* R.M.Schust. (Schuster and Engel, 1974, fig. 1) and *Hygrolembidium triquetrum* J.J.Engel & R.M.Schust. (Schuster and Engel, 1987a, fig. 13). In these species, however, branching is exclusively intercalary, or nearly so. In *K. calcarata*, the erect, pinnately decompound branches are terminal in origin (both *Frullania* and *Microlepidozia* types), arising at regular intervals from a ± elongated, indeterminate, leafy "runner."

Optimally developed plants of *Kurzia compacta* show a clear approach to the complex pattern of gametophyte organization seen in subg. *Dendrolembidium* (Schuster, 1980a, p. 382). They have erect, brownish axes that are distally green and compactly bipinnate, while the lower parts of the erect main axis bear long, sometimes ramified, microphyllous flagelliform, root-like axes. Unlike *K. tenax*, however, leaf bases are never armed with tapered, multicellular, abaxially projecting processes.

Subg. ***Dendrolembidium*** (Herzog) Grolle

Dendrolembidium Herzog, Ark. Bot., ser. 2, 1: 497. 1951 (preprint; 1952, journal).
Kurzia subg. *Dendrolembidium* (Herzog) Grolle, J. Jap. Bot. 39: 80. 1964. Lectotype: *Kurzia tenax* (Grev.) Grolle.

Kurzia tenax (Grev.) Grolle

Jungermannia tenax Grev., Ann. Lyceum Nat. Hist. New York 1: 277. *pl. 23*. 1825. *Lepidozia tenax* (Grev.) Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 212. 1845. *Mastigophora tenax* (Grev.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. *Lembidium tenax* (Grev.) Steph., Sp. Hepat. 3: 365. 1908. *Dendrolembidium tenax* (Grev.) Herzog, Ark. Bot. N.S. 1: 499. 1951. *Kurzia tenax* (Grev.) Grolle, Rev. Bryol. Lichénol. 32: 174. 1964 (1963). Type: Australia, *Fraser*, ex herb. Kew (G!).

Plants vigorous, in tufts or in loose, caespitose masses, with a ± distinct, creeping rhizome giving rise to long, microphyllous, root-like, often ramified geotropic axes and to stiffly erect, complex, photosynthetic systems, the erect, dendroid shoot system olive-to-brownish green to light green (principal axes usually remaining green, but somewhat whitish and translucent), the branches cernuous to (particularly when dry) circinate. Branching of the aerial shoot system decompound, 2–3-pinnate, the branches normally all terminal, dendritic, formed by ± regular alternation of *Frullania*- and *Microlepidozia*-type branches; half-leaf of *Frullania*-type branches 2-lobed to 0.7; first branch underleaf 2–3-lobed, inserted on ventral-lateral side of branch at juncture of stem and branch. Stem below primary branches with a large-celled hyaloderm of 16–20 colorless, echlorophyllose, very large cells, not collapsing with age; medulla of 7–10 rows of thin- to weakly firm-walled cells, without a differentiated thick-walled subcortex. Leaves of aerial photosynthetic system ca. 725–750 μm wide × 625–650 μm long, broadly oblong to oblong-quadrate, transversely to feebly succubously inserted, 5–7-lobed, divided to 0.6–0.7. Lobes slender, long-acuminate, occasionally with a basal tooth, the lobes 4–6 cells wide at base, ending in a uniseriate row of (4)5–6(7) cells, the cells of uniseriate row 36–48 × 48–62(72) μm. Disc 6–8 cells high, the margins appendiculate, bearing cilia and laciniae, some tortuous or recurved; leaf bases, along the entire, almost straight line of insertion, bearing copious, crowded, finger-like cilia or appendages directed toward stem base, the appendages to 12 cells long. Leaves of primary branches somewhat simpler than those of main stems, 4–5-lobed with disc margins less ciliate-laciniate, the appendages of the leaf base fewer and less well developed; leaves of secondary axes usually simply 4-fid, subtransversely inserted and oriented, without basal appendages. Cells of disc-middle rather thick-walled, strongly chlorophyllose, small, 13–17 × 16–25 μm up to 21–25 × 23–30 μm; surface of

median and upper cells strongly and closely papillose, the cells of lobes somewhat more strongly papillose; basal cells and cells of appendages smooth or striolate, appearing less chlorophyllose than median and distal cells. Oil-bodies (Schuster, 1980a) of basal cells (at least on branch leaves and some cells of the filiform appendages) minute, present in a minority of cells, 0–1(2–3) per cell, glistening and homogeneous to obscurely 2–3 segmented, ca. 2.5–3 × 3.3–4 μm; cells of lobes uniformly oil-body free. Underleaves leaf-like, ca. 0.7–0.85 as large as leaves, symmetric, usually 5–6-lobed to 0.65–0.8, the lobes narrower than on leaves, sublinear, often ending in slime papillae; disc lower than on leaves, armed at juncture with stem with a "comb" of appendages similar to those of the leaves. Asexual reproduction absent.

Androecia on abbreviated, spicate branches from bases of the erect, leading leafy axes or (sometimes) from rhizomatous leading axes. Gynoecia on short ventral-intercalary branches, isophyllous; bracts and bracteoles erect, isophyllous, lacking appendiculi, sheathing the perianth base, ovate-lanceolate, unlobed or very shallowly bilobed, formed of elongate, pellucid, leptodermous cells, the margins entire to vaguely crenulate by slightly projecting, rounded apices of the strongly elongated marginal cells; bracteoles identical to bracts. Perianth hyaline, elongate-fusiform, very slender, about 0.6–0.75 emergent, the distal portion bluntly 3-plicate; mouth gradually narrowed, lobulate, the lobes fringed with tapered, narrow (mostly 5–8:1) cells, often sigmoidal, free only at their often arcuate apices; perianth at least locally 2-stratose proximally.

Seta with 8 rows of very large epidermal cells surrounding ca. 18 rows of much smaller, internal cells. Capsule long-ovoid-cylindrical, 575–600 μm wide × 1750–1900 μm long, the wall 3-stratose, very thin (for capsule size), 28–30 μm thick, the outer layer about equal to the combined thickness of the two inner layers; outer layer of cells with two-phase development, the primary cell walls developing almost quadrate "primary cells" devoid of thickenings, longitudinally subdivided by one wall that bears sinuous-nodular thickenings forming irregular brownish sheets of radial walls; innermost layer of cells with numerous rather weak, but closely spaced, narrow and delicate semiannular bands, appearing as tangential bands in surface view.

Spores 10–12 μm in diam., yellow-brown to pale brown, the spore wall rather thin, delicately closely, vermiculate and verrucate, the vermiculae anastomosing to some extent, but not delimiting areolae. Elaters 11–12.5(13) μm in diam., rather straight and moderately thinner at the ends, bispiral, the spirals 3–4 μm wide.

Distribution and Ecology: New Zealand: Auckland Islands (15–45 m), Stewart Island (5–200 m), South Island (2–280 m); Australia: Tasmania, southeast Australia.

In the South Island only in southwestern sector, including Fiordland, Southland and Westland, with its northern limit on the Paparoa Ra. In low-lying bogs dominated by *Halocarpus bidwillii* and *Empodisma minus*, and associated often with *Riccardia cochleata* (Schuster, 1980a). The species has a similar ecology to *Kurzia calcarata* and *K. helophila*. On Stewart Island (Fern Gully Track) forming pure colonies on very old rotting logs and on the forest floor in a forest dominated by *Fuchsia excorticata* and *Griselinia littoralis* canopy and a *Blechnum discolor* understory. Also in a bryophyte-covered mass of tree roots in an open podocarp–hardwood forest including *Dacrydium cupressinum* and *Weinmannia racemosa* with a subcanopy of *Dicksonia squarrosa* and the woody liana *Ripogonum scandens* (Port Pegasus). On Awarua Bog (Southland, near sea level) it is found under *Pteridium esculentum* and *Baumea tenax*. In forest sites it is found with *Bazzania adnexa*, *B. nitida*, *Kurzia hippuroides*, *Pyrrhobryum bifarium*, *Rhizogonium distichum*, *R. pennatum*, *Riccardia crassa* and *Telaranea tetrapila*.

Comments: *Kurzia tenax* differs from the Tasmanian species *K. dendroides* in the long-acuminate leaf lobes, ending in a uniseriate row of (4)5–6(7) cells; the smaller leaf cells (20–30 × 22–36 μm vs. 36–55 × 55–75 μm in *K. dendroides*), clearly smaller than the elongated cells of the uniseriate lobe apices; and the more numerous appendiculi of the stem leaves.

Grolle (1964d, p. 80) placed *Kurzia tenax* into subg. *Dendrolembidium* with *Megalembidium*, also a dendroid genus with superficially similar organization (see also Engel and Braggins, 2005). As noted under *Megalembidium*, the two differ in numerous features—most obviously in the absence of a comb of appendiculi at the leaf bases in *Megalembidium*.

Psiloclada Mitt.

Psiloclada Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 143. 1855.
Lepidozia subg. *Apiculo-lepidozia* S.W.Arnell, Bot. Not. 107(4): 429. 1959.

Plants wiry, loosely prostrate to somewhat ascending, dull, olive-green to brownish green, minute. Branching irregularly pinnate to rather regularly (but not especially closely) 1–2-pinnate, the branches of the *Frullania* type, oriented at ± 90° to main axis; ventral-intercalary branches occasional, often becoming flagelliform. Stem rigid, rather large for plant size, the cortex ill-defined, of notably thick-walled cells that grade into the thick-walled medullary cells, the medullary cells somewhat less thick-walled toward the central portion. Leaves remote to ± contiguous, hand-like and cupped: the disc and lobe bases stiffly spreading laterally, the terminal setiform cells each erect and oriented at ± right angles to the disc or aligned toward stem, the leaf insertion transverse in dorsal half and attaining the stem midline, distinctly succubous in ventral half; leaves weakly to strongly asymmetrically obtrapezoidal, 5–9(10)-lobed to 0.6–0.8; branch leaves with 1(2) fewer lobes. Lobes asymmetric, the ventral lobe(s) larger than the dorsal, the lobe bases each comprised of a few, thick-walled cells similar to those of the disc, the lobes each ending in a single, stiff, setiform, finger-like, hyaline, echlorophyllous, thin-walled cell, 11–12 μm wide × 40–65 to 85–110 μm long. Disc asymmetric, 1–2 cells high dorsally, 3–5 cells high ventrally. Cells of disc and lobe bases densely chlorophyllose, thick-walled; surface smooth. Oil-bodies absent. Underleaves remote, 3–6(8)-lobed, the disc stiffly spreading (often at right angles to the stem), the setiform cells each strongly erect and oriented parallel to stem or arched toward the stem, the lobes consisting solely of a single hyaline, elongate, setiform cell or of 2 cells, then the terminal setiform cell subtended by a subisodiametric cell; disc usually 2 cells high. No asexual reproduction.

Dioecious (but often sterile). Androecia on short, determinate, ventral-intercalary branches from leading shoots; bracts 4-lobed to ca. 0.5, the terminal cell very long and narrow; antheridia 1–2 per bract, the stalk uniseriate; bracteolar antheridia lacking. Gynoecia on abbreviated ventral-intercalary branches from main stem, the gynoecium base narrowly stipitate (with a rudimentary perigynium) and rhizoidous, the gynoecium with 1–2 series of bracts and bracteoles, the innermost ± ovate, irregularly 2–4-fid for 0.5–0.7 their length, the disc broadly orbicular-quadrate; lobes acuminate-caudate, ending in 1–3 exceedingly elongate cells. Perianth narrowly fusiform to slenderly ovoid, terete below, trigonous above, distinctly pluriplicate distally, ± gradually narrowing to the contracted mouth; mouth fringed with ± tortuous cilia consisting of a single elongate cell or a uniseriate row of 2 elongate cells and, immediately below, 1–2 biseriate tiers comprised of laterally connate cells free at their apices, the cilia also with a few accessory shorter teeth below; perianth 2–4-stratose in basal sector.

Seta with 8 rows of outer cells surrounding an inner core of 13 much smaller cells. Capsule

short-ellipsoidal, the wall 2(very locally 3)-stratose; outer layer of cells with two-phase development, the longitudinal walls with thin, sheet-like thickenings and feebly nodule-like swellings (lending the vertical walls a sinuous-nodular appearance) alternating with walls that are devoid of thickenings; inner cells longer and narrower, for the most part with rather nodule-like to spine-like thickenings, sporadically tangentially extended and then with incomplete to complete semiannular bands.

Spores 11–14 μm in diam., vermiculate-irregularly areolate. Elaters 8.2–12.5 μm wide, bispiral.

Type: *Psiloclada clandestina* Mitt.

Psiloclada is likely a monotypic genus, with a single, variable, broadly distributed species that may be subdivided into three subspecies (Schuster, 1980a, 2000a). Subspecies *clandestina* occurs in New Zealand, Tasmania and Australia; subsp. *melanesica* R.M.Schust. is found in New Guinea, New Caledonia, the Solomon Islands and Fiji (and ?Amboina); and subsp. *spinosa* (S.W.Arnell) R.M.Schust. is disjunct in South Africa (Arnell, 1954, type of *Lepidozia spinosa*; 1963). The status of *P. unguiligera* Schiffn. of Indonesia, Melanesia and the Philippines is uncertain and may be the same as subsp. *melanesica*.

References: Fulford and Taylor (1959); Engel (1985); Schuster (1980a, 2000a).

Psiloclada clandestina Mitt.

Psiloclada clandestina Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 143. *pl. 99, f. 4.* 1854. Type: New Zealand, North Is., Wellington, *Stephenson.*

Only the typical subspecies occurs in our area.

Psiloclada clandestina Mitt. subsp. ***clandestina***

[Plate 7A, B; Fig. 82]

Psiloclada clandestina subsp. *clandestina* fo. *major* R.M.Schust., J. Hattori Bot. Lab. 48: 411. 1980, *syn. nov. Psiloclada major* (R.M.Schust.) J.J.Engel, Phytologia 58: 324. 1985. Type: New Zealand, South Is., Westland Prov., Haast Pass, *Schuster 59641.*

Plants filamentous and thread-like in smaller phases to leafy in aspect in vigorous phases, with wiry, rigid, brittle axes; shoots to 345 μm wide with leaves. Branches remote and irregularly pinnate to frequent, distinctly and regularly 1(2)-pinnate, the terminal branches frequently becoming flagelliform; branch half-leaf 4(5)-lobed; first branch underleaf 2–3-lobed. Rhizoids rare, lacking in distal shoot sectors. Leaves rigid, firmly attached, 120–175 μm wide × 100–175 μm long, on main stems (5)6–9(10)-lobed, moderately asymmetrical, the ventral 1–2 lobes larger, formed of 2–3 to 4–5 cells, the dorsal smaller, usually 1(2)-celled. Lobes each ending in a highly differentiated, erect, unicellular, conspicuously elongated, hyaline, rigid, setose apical cell, the apical lobe cell directed toward stem apex or inclined toward stem, basally often a little dilated and bulb-like, long-tapered, 10–12 × 84–110 μm. Disc asymmetrical, 2 cells high in dorsal half, to 4–5 cells high in ventral half, the disc 10–16 cells wide at base. Cells of disc and lobe bases thick-walled, small, the median disc cells 12–17 × 15–19 μm. Oil-bodies absent, but a few droplets present in some disc cells, when present, obscure,

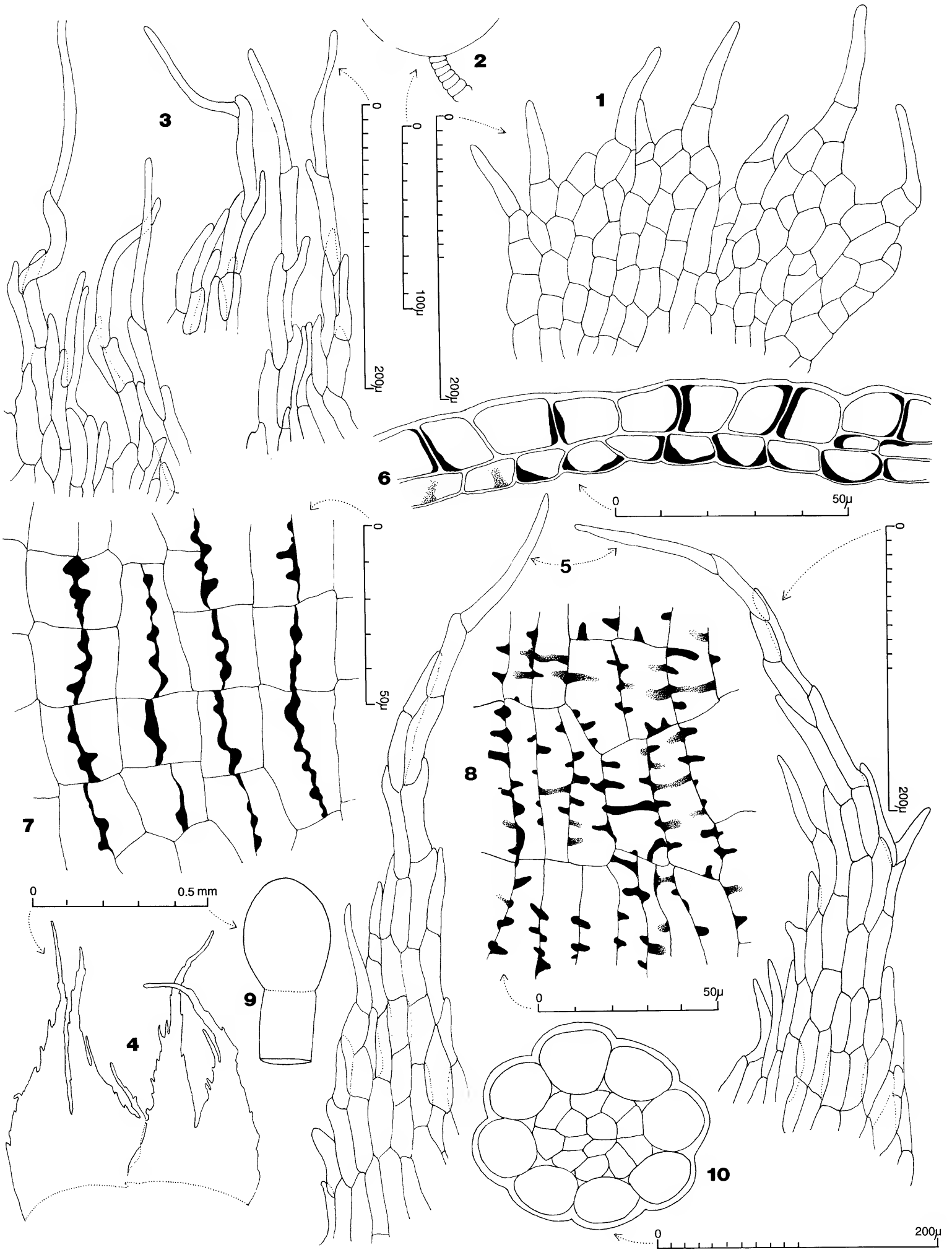

Fig. 82.
Psiloclada clandestina Mitt. 1. ♂ Bract. 2. Antheridium. 3. Portion of perianth mouth. 4. ♀ Bracts. 5. Distal portions of ♀ bract. 6. Capsule wall, cross section. 7. Capsule wall, outer layer. 8. Capsule wall, inner layer. 9. Capsule profile. 10. Seta, cross section. (Fig. 1, from *Engel 6566*, New Zealand, South Is., Westland EP, Mt. Hercules Scenic Reserve; 2, from *Hatcher 820*, New Zealand, South Is., Westland EP, Martins Bay; 3–10, from *Engel 18326*, New Zealand, South Is., Westland EP, Arthur's Pass Natl. Park, N of Kellys Creek.)

1–2(3) per cell, hyaline, homogeneous or consisting of a few obscure inconspicuous spherules, much smaller than chloroplasts. Oil-droplets of stem cortex cells 0–5(7) per cell, homogeneous, colorless, 0.75–1.5 μm in diam., ellipsoidal or spherical or an irregular variant on spherical. Chloroplasts very large for cell size, in disc and all lobe cells except the long curved tip cell, which is devoid of contents. Underleaves of main stems (3)4–6(8)-lobed, the lobes usually consisting of a basal cell and a setose apical cell; disc rudimentary, spreading, 2 cells high. Fungal partner an ascomycete.

Androecia on abbreviated, tightly spicate branches from leading shoots; bracts ventricose, the lobes acuminate, terminating in a uniseriate row of 2–3 cells, the terminal cell very long and narrowing toward the tip, the lobe bases crenate-denticulate; margins of disc sparingly crenate-dentate, devoid of slime papillae. Gynoecia with bracts of innermost series much larger than leaves, erect and closely ensheathing the perianth but often with diverging lobes, the bracts concave, bifid; lobes caudate, the tip consisting of a uniseriate row of 2–3 very elongate cells, the lobe margins crenate-denticulate often by the variously projecting distal end of lobe cells; lamina composed of irregularly short- to long-rectangular, leptodermous cells, the margins sparingly crenate-dentate; bracteole similar in size and form. Perianth rather inconspicuous *in situ* yet rather large for plant size, straight to curved; mouth with cilia each consisting of a single elongate cell or a uniseriate row of 2 elongate cells (ca. 9–12 × 120–150 μm), the distal end of the penultimate cells often projecting and forming a shoulder-like process.

Capsule wall 2(very locally 3)-stratose, 16–20 μm thick, the outer layer 1.4–1.6× thicker than inner layer; outer layer of cells feebly tiered, ca. 28–34 × 45–48 μm, ± regularly short-rectangular, the alternating walls with thin, sheet-like thickenings and feebly nodule-like swellings lending the vertical walls a sinuous appearance, the transverse walls devoid of thickenings; innermost layer of cells longer and narrower, 8–12 × 45–75 μm, mostly with nodule-like to spine-like thickenings, with complete semiannular bands sporadic and often non-pigmented in median sector.

Spores 12.5–13.9 μm in diam., with a network of low, often furcate ridges that often anastomose to form irregular and weak areolae. Elaters 8.2–8.6 μm wide, feebly to moderately tortuous, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–3.4 μm wide.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island, South Island (0–660 m), North Island (200–580 m), Chatham Islands; Australia: Tasmania, Victoria. In New Zealand known from Fiordland, Westland, Western Nelson, Marlborough, Southern North Island, Volcanic Plateau (Lake Rotoehu), Taranaki (Mt. Taranaki), Auckland (Mt. Moehau) and Northland (Waipoua Forest) EPs. Very common in lowland forests of Westland and Fiordland, but the comparatively few collections from the North Island suggest it is relatively uncommon there.

In pure mats or woven through other bryophytes, on rotting wood and tree roots, humic soil, occasionally seen hanging in wefts from soil and other bryophytes, occasionally on rock surfaces. In the North Island usually on or at base of tree-fern trunks (with *Calomnion complanatum*, *Bazzania tayloriana* and *Trichomanes venosum*); rarely epiphyllic (on *Hymenophyllum ferrugineum*). Found under lowland to montane forest, mainly under lowland forests of *Dacrydium cupressinum*, *Weinmannia racemosa*, *Quintinia serrata*, *Metrosideros umbellata*, under *Nothofagus solandri* and *N. menziesii* forest, or under *Lepidothamnus intermedius* forest. Found most constantly in association with *Bazzania nitida*, *Zoopsis argentea* and *Rhizogonium pennatum*. Other species that sometimes occur with *Psiloclada* are *Acrobolbus lopho-*

coleoides, *Acromastigum anisostomum*, *A. colensoanum*, *A. marginatum*, *Bazzania hochstetteri*, *B. monilinervis*, *B. novae-zelandiae*, *Clandarium xiphophyllum*, *Distichophyllum pulchellum*, *Ditrichum punctulatum*, *Heteroscyphus billardierei*, *H. decipiens*, *Kurzia hippuroides*, *Lembidium longifolium*, *Lepicolea scolopendra*, *Lepidozia kirkii*, *L. concinna*, *L. spinosissima*, *Leucobryum candidum*, *Marsupidium knightii*, *Podomitrium phyllanthus*, *Rhizogonium distichum*, *Riccardia cochleata*, *R. crassa*, *Saccogynidium australe*, *S. decurvum*, *Schistochila glaucescens*, *S. nobilis*, *Telaranea tuberifera*, *Trichomanes venosum*, *Trichotemnoma corrugatum*, *Tylimanthus diversifolius*, *Zoopsidella caledonica*, *Zoopsis bicruris*, *Z. ceratophylla*, *Z. leitgebiana*, *Z. matawaia* and *Z. setulosa*.

Comments: *Psiloclada clandestina* is here defined to include plants that are variable in vigor, leaf lobe number and underleaf lobe number. Smaller phases are filamentous in aspect and have 5–6 leaf lobes and 3–4 underleaf lobes. This is the phase regarded as *P. clandestina* fo. *clandestina* in Schuster (1980a) and *P. clandestina s. str.* in Engel (1985). Subsequent detailed studies of New Zealand populations have revealed that a single species occurs within here and that an increase in vigor is coupled with an increase in the number of leaf and underleaf lobes. Particularly vigorous plants have leaves 8–9 to even 10-lobed and underleaves 5–6(8)-lobed; such plants are often leafy in aspect. This phase was recognized taxonomically as *P. clandestina* subsp. *clandestina* fo. *major* in Schuster (1980a) and as a distinct species, *P. major*, in Engel (1985).

In the field, *Psiloclada clandestina* may be recognized by the minute size, the very slender, wiry plants with tiny and mostly remote leaves with lobes stiffly oriented toward the shoot apex and by the dull olive-green or brownish green color.

Subfam. ***Drucelloideae*** (Boesen) R.M.Schust.

*S*ubfamily *Lepidozioideae* tribe *Drucellae* Boesen, Lindbergia 8: 78. 1982. *Lepidoziaceae* subfam. *Drucelloideae* (Boesen) R.M.Schust., Phytologia 56: 69. 1984.

Drucella E.A.Hodgs.

Drucella E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 2: 45. 1962.

Plants strongly anisophyllous, light green to whitish green, weakly chlorophyllose and devoid of wall pigments, nitid, to 0.45 mm wide. Plants with an extensive system of basal, creeping, plagiotropic, small-leaved, often microphyllous, strongly elongated, occasionally branched rhizomatous or stoloniform axes from which arise ascending to erect, often arched, simple or sporadically branched leafy shoots of limited length. Branching irregular, uniformly intercalary, the branches mostly lateral, exceptionally ventral. Stem rigid and wiry, the cortical cells in surface view strongly elongated, ± tiered, the longitudinal walls very thick, the transverse ones thin, in cross section in 6–10 rows; medulla of 5–9 rows of rather thick-walled cells of ± similar diameter to the cortical cells. Rhizoids occasional, the tips often swollen, at underleaf bases of older sectors of shoots, also from bases of leaves and underleaves of rhizomes or stolons. Leaves contiguous to weakly imbricate, stiffly and widely spreading, 160–250 μm wide at the lobe apices, 100 μm wide at the leaf base, 270–325 μm long, separated by 1–3 cortical cells on either side, the insertion clearly incubous, not reaching stem midline dorsally and delimiting a leaf-free strip of 2 rows of cortical cells; leaves asymmetrically

cuneate to narrowly obtrapezoidal, rather narrowed to the insertion, (2)3-fid to 0.5–0.75. Lobes usually unequal, entire, the dorsal lobe linear-lanceolate, 2–3(4) cells wide at base, terminating in a uniseriate row of 2–4 moderately elongated cells, the middle lobe similar to the dorsal or a little smaller, the ventral lobe usually smaller, often only 1–3-celled and at times ending in a slime papilla. Disc mostly 2–3(4) cells high, (5)6 cells wide at the base. Cells of disc cells pellucid, equally very thick-walled and without trigones, the middle lamella conspicuous, the median cells 20–25 μm wide × 30–35 μm long; surface smooth. Oil-bodies absent or occasionally 1 or 2 per cell, spherical, moderately but faintly granular, ca. 5 μm in diam., breaking up rapidly to oil-droplets that are homogeneous, small, 1.8–2.3 μm in diam. Chloroplasts few. Underleaves inserted on 2–3 rows of stem cells, narrower than stem and leaving the stem broadly exposed, distant, small, spreading to squarrose, ± obtrapezoid-quadrate, 2–3-lobed, the lobes often unequal, consisting of 1–2 cells, terminating in a slime papilla; the disc 1–2.5 cells high and 3 cells wide. Asexual reproduction absent.

Dioecious. Androecia typically on short ventral-intercalary branches, rarely on lateral-intercalary branches; bracts slightly larger than vegetative leaves, strongly concave, bifid to 0.5–0.7; antheridia 1 per bract, the stalk uniseriate. Gynoecia typically on short ventral-intercalary branches, exceptionally on short lateral-intercalary branches; bracts in 2–3 series, appressed to perianth, (2)3–5-fid to 0.5–0.7, the lobes 2–4 cells wide at base, terminating in a uniseriate row of 5–7 cells, the lobes with a few teeth below, the distal sector of lobes ciliiform; bracteoles similar to bracts but somewhat smaller and sparingly armed. Perianth ovoid-cylindrical, the mouth wide, lobulate-ciliate, the cilia terminating in a uniseriate row of 4–8 elongated cells, with accessory teeth below; perianth unistratose throughout and with cell walls thinner than those of leaf cells.

Seta with 8 rows of outer cells surrounding an inner core of 14–16 much smaller cells. Capsule short-ovoid, small, the valves only 140–145 × 315–330 μm, the wall 14–15 μm thick, bistratose, the outer layer somewhat thicker than the inner; outer layer of cells distinctly tiered, comprised of only 6–7 tiers (the large basal cells at valve base excepted), the cells long-rectangular, the development of the outer layer not fixed and of two types: a) one with two-phase development, the longitudinal walls with pale magenta, well-defined, sheet-like, continuous thickenings + nodule-like thickenings (lending a sinuous appearance) alternating with walls that are devoid of thickenings (or with a very few, sporadic, local, non-pigmented, nodular swellings), the transverse walls devoid of thickenings; and b) the other type with one-phase development, all longitudinal walls with thickened continuous sheets of pigmented material and (*fide* Boesen, 1982) with semiannular bands common; innermost layer of cells markedly long and narrowly rectangular, the longitudinal walls with thick continuous sheets of material, with semiannular bands common or with complete, well-developed bands present but less frequent, the longitudinal walls then with nodular thickenings that variously extend onto the exposed tangential wall as feeble spurs or weak, faintly pigmented incomplete or complete semiannular bands.

Spores 8.6–9.6 to 11–13.2 μm in diam., reddish brown or yellow-brown, finely reticulate. Elaters rigid, 8.2–9.6 to 11–16 μm wide, slightly tapered to tips, bispiral, the spirals 2.4–2.9 μm wide.

Type: *Drucella integristipula* (Steph.) E.A.Hodgs. (≡ *Lepidozia integristipula* Steph.)

The genus is monotypic and known only from New Zealand, Tasmania and southeast Australia.

References: Boesen (1982); Hodgson (1962b); Schuster (1980a, 2000a).

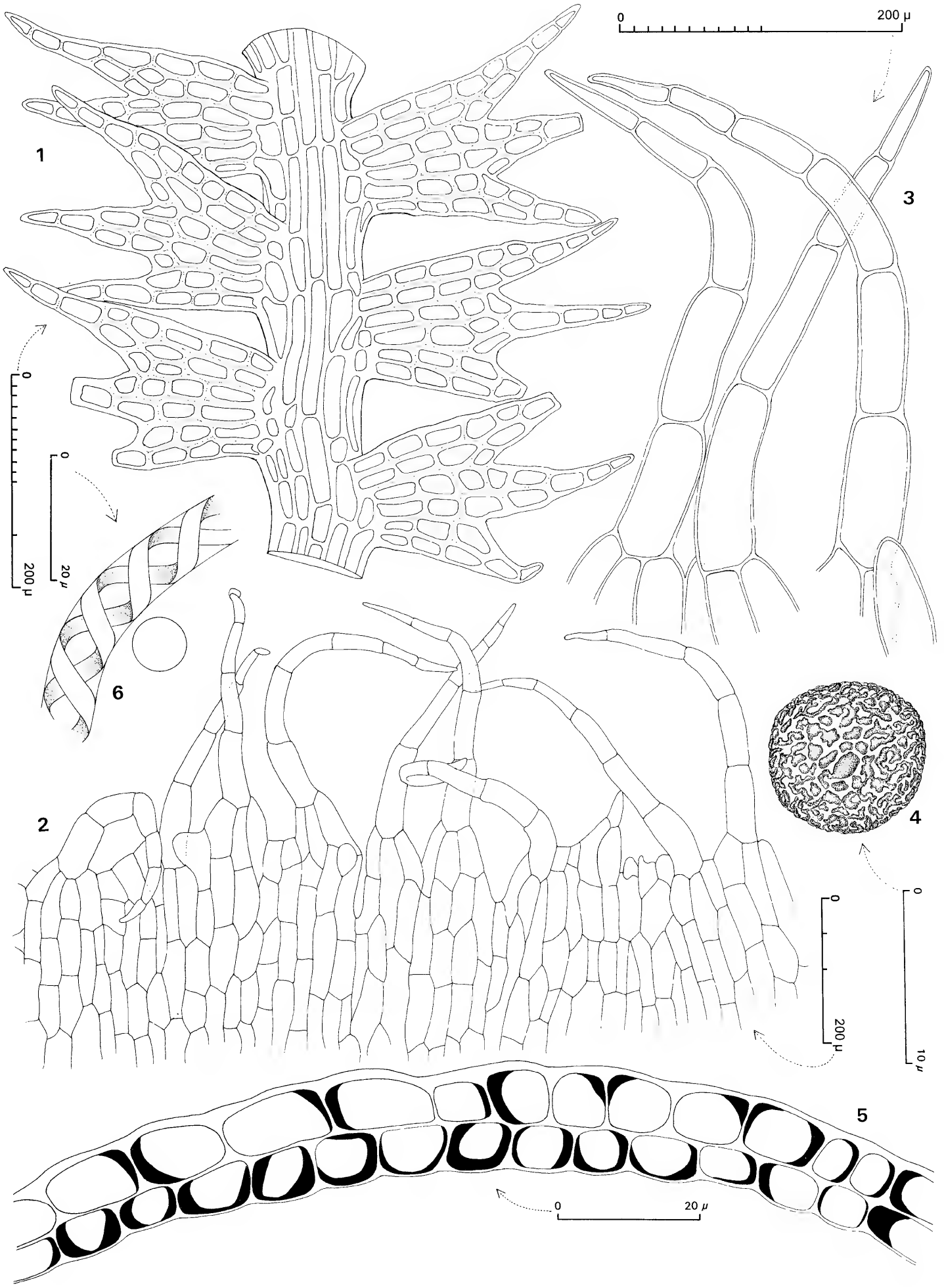

Fig. 83.
Drucella integristipula (Steph.) E.A.Hodgs. 1. Portion of main shoot, dorsal view; note the thick-walled leaf cells, the leaf-free strip and the long, thick-walled cortical cells. 2. Portion of perianth mouth. 3. Cilia of perianth mouth. 4. Spore. 5. Capsule wall, cross section. 6. Sector of elater and spore outline drawn to same scale. (Fig. 1, from *Engel 23612*, New Zealand, North Is., Volcanic Plateau EP, Kaimai-Mamaku Forest Park, Kaimai Ra., Aongatete R.; 2–6, from *Glenny 9261*, New Zealand, South Is., Western Nelson EP, Pupu Walkway.)

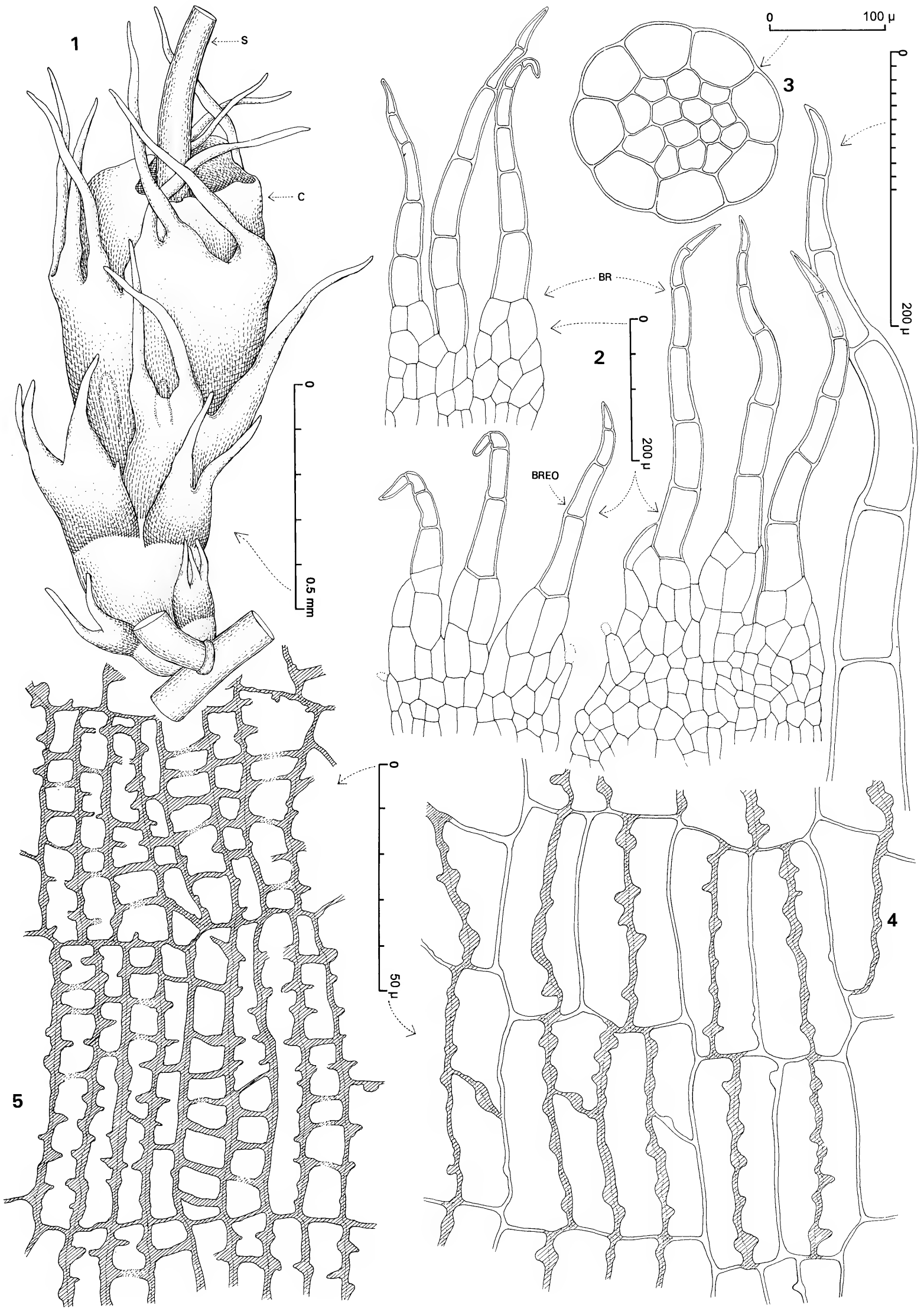

Fig. 84.
Drucella integristipula (Steph.) E.A.Hodgs. 1. Mature gynoecium originating from a stoloniform axis; note long calyptra (= C) and presence of unfertilized archegonia (stippled) carried partway

Drucella integristipula (Steph.) E.A.Hodgs.

[Plate 7C; Figs. 83, 84; Fig. 85: 2, oil-bodies, p. 394]

Lepidozia integristipula Steph., Sp. Hepat. 6: 331. 1922. *Drucella integristipula* (Steph.) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 2: 45. 1962. Lectotype (*fide* Boesen, 1982): New Zealand, Great Barrier Is., *Kirk 201* (MPN Hodgson herb. no. 783, *non vidi*); isolectotype: (CHR!).

See genus description.

Distribution and Ecology: New Zealand: South Island (300–1000 m), North Island (200–640 m); Australia: Victoria, Queensland. For comments on distribution see Boesen (1982). With a local and rather sporadic distribution in New Zealand. In the North Island known from Southern North Island (Akatarawa Valley), Auckland (Coromandel Peninsula, Kaimai-Mamaku Forest Park, Cascade Kauri Park and Great Barrier Island), several stations in Northland EP (including Waipoua Forest, Mataraua Forest, Omahuta Forest and Mangamuka Gorge Reserve). In the South Island known from only two sites, both in Western Nelson province (Wangapeka River and Croesus Track).

For the most part in exposed sites or at times in partial shade, over fine-grained, water-retentive, compact soils in areas with disturbed habitats such as on roadside banks and clayey banks along tracks. Also on the forest floor under sparse *Agathis australis* canopy (Cascade Kauri Park). In the Mataraua Forest on exposed heavy, orange, stone-filled clay of dripping banks formed by quarrying activity. At this site the banks are overshadowed by *Blechnum novae-zelandiae*, under *Metrosideros robusta – Weinmannia silvicola – Prumnopitys ferruginea* forest and associated with *Acromastigum colensoanum*, *Kurzia compacta*, *Lepidozia spinosissima*, *Paracromastigum furcifolium*, *Psiloclada clandestina*, *Saccogynidium australe* and *Zoopsis setulosa*. At Kaimai-Mamaku Forest Park on vertical banks beneath a dense overhang of *Freycinetia baueriana* and *Blechnum* in a stream valley under an open canopy of *Beilschmiedia tawa* and *Weinmannia silvicola*. At Akatarawa Saddle (Tararua Ra., 500 m) on the soil B-horizon in an open road cutting through regenerating *Weinmannia racemosa* scrub, under *Blechnum novae-zelandiae* with *Ditrichum difficile*, *Haplomitrium gibbsiae*, *Isotachis lyallii*, *Jackiella curvata* and *Polytrichum juniperinum.* On the Croesus Track (Paparoa Ra., 300 m) on a track cutting under regenerating *Dacrydium cupressinum – Weinmannia racemosa* forest, with *Brevianthus flavus*. In the Wangapeka Valley (near Kiwi Saddle, 1000 m) on an overhanging track cutting under *Nothofagus menziesii – Dracophyllum longifolium* forest with *Diplophyllum dioicum*, *Haplomitrium gibbsiae* and *Solenostoma totipapillosum*.

Comments: The combination of incubous leaves, absence of terminal branching and a leaf-free strip of stem cells will distinguish *Drucella* from all other lepidozioid hepatics.

Boesen (1982) stated that the outer layer of the capsule wall has pigmented thickenings on all longitudinal walls, with each cell having 6–10 semiannular bands (i.e., with a one-phase development). The capsule in *Glenny 9261* (CHR, F), however, is rather different. In this

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up the calyptra surface (S = seta). A short intercalary branch (only the branch base included) with an unfertilized gynoecium which was removed for clarity. 2. ♀ Bracts (= BR) and bracteole (= BREO) from innermost series, and, to right, a lobe at higher magnification. 3. Seta, cross section. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. (Figs. 1, 2, 4, 5, from *Glenny 9261*, New Zealand, South Is., Western Nelson EP, Pupu Walkway; 3, after Boesen, 1982.)

population the outer layer has a two-phase development (though somewhat imperfect), with alternating longitudinal walls having pigmented, continuous sheets of thickening and nodule-like swellings that lend a sinuous appearance (Fig. 84: 4). These walls alternate with those that are devoid of thickenings or have local, non-pigmented, low swellings (Fig. 84: 4). The outer layer lacks semiannular bands. Also, semiannular bands of the inner layer of the capsule wall in the Glenny plant are less frequent than those described and illustrated by Boesen (1982, see fig. 7: 3). In the Glenny plant nodular thickenings are frequent and these variously extend on to the exposed tangential wall as feeble spurs or weak, faintly pigmented nearly complete or complete semiannular bands (Fig. 84: 5) and careful focusing is required to observe the weak bands.

Subfam. ***Bazzanioideae*** Rodway

Subfamily *Bazzanioideae* Rodway, Tasman. Bryoph. 2: 23. 1916.

Acromastigum A.Evans

Acromastigum A.Evans, Bull. Torrey Bot. Club 27: 103. 1900.

Plants subisophyllous to markedly anisophyllous, ± stiff and wiry, prostrate to suberect, at times with yellowish to reddish brown pigments, small to medium. Branching frequent, often but at times not uniformly pseudo-dichotomous, never pinnate, the branches of *Frullania* type, often originating from only one side of axis, subequal to main axis in vigor and with the main axis losing its dominance; branch half-leaf undivided, positioned in the fork of each "dichotomy"; *Acromastigum*-type branches present, stoloniform, the half-underleaf to one side at branch base. Ventral-intercalary branches also present, stoloniform, geotropic. Stems usually rigid and wiry, the cortex in 6–8 rows, in a number of species consistently 7, in some species 14–16, the cells larger than the medullary, with firm to thick walls; medulla in many rows of rather firm- to thick-walled cells (in only 3 rows in *A. rigidum* R.M.Schust.). Rhizoids from cells of underleaves and leaves of stoloniform branches. Leaves with insertion transverse to distinctly incubous (rarely slightly succubous), inserted to stem midline dorsally, with apices often variably deflexed, undivided or bidentate to bilobed (rarely 3-dentate), the ventral lobe or tooth often longer than the dorsal. Cells with walls slightly to distinctly thickened, with trigones at times nodulose, with a vitta of elongated, differentiated cells present in some species; surface smooth or papillose. Oil-bodies papillose or coarsely botryoidal or homogeneous and then 1(2) per cell. Underleaves with shape and form ± similar to the leaves or more commonly clearly differentiated, undivided or 2–3-dentate, the teeth often reduced to slime papillae. Asexual reproduction lacking, or occasionally by caducous leaves in a few species.

Dioecious. Androecia on short, determinate, tightly spicate ventral-intercalary branches from leading shoots or from geotropic stoloniform axes; bracts strongly ventricose, usually bidentate to bifid; antheridia 1 per bract, the stalk biseriate; bracteoles concave, usually bidentate, sporadically with antheridia. Gynoecia on abbreviated ventral-intercalary branches; bracts of innermost series much larger than leaves, ovate, variously dentate, laciniate or lobate but typically with 2 main segments; bracteole similar in size and form. Perianth ± fusiform, terete below, trigonous above, the distal sector pluriplicate and narrowing to the contracted mouth, the mouth lobate or laciniate-ciliate; perianth unistratose throughout or 2-stratose in basal sector.

Seta with 8–16 rows of outer cells surrounding an inner core of numerous, much smaller

cells. Capsule ovoid, the wall 2–4-stratose; outer layer of cells with two-phase development, the alternating longitudinal walls with nodular and often confluent thickenings lending them a ± sinuous appearance; innermost layer of cells with semiannular bands complete or at times incomplete, the bands at times forked, the radial walls also sometimes with nodular thickenings.

Spores minutely papillose or papillose-vermiculate. Elaters bispiral.

Type: *Acromastigum integrifolium* (Austin) A.Evans (≡ *Mastigobryum integrifolium* Austin)

Acromastigum is a genus of 35–40 species (Schuster, 2000a). In the New World it occurs only in southern South America, with three species—*A. laetevirens* (Sande Lac.) A.Evans, *A. anisostomum* and *A. cunninghamii*, the latter two of which also occur in our area (see Fulford, 1966; Grolle, 1961d). One species, *A. exile* (Lindenb.) A.Evans, is present in South Africa (Arnell, 1963). Ten species occur in New Guinea (Grolle & Piippo, 1984). One species, *A. integrifolium*, the type of the genus, occurs in Hawaii. Eight species occur in New Zealand.

The two genera comprising the *Bazzanioideae* may be differentiated by several characters. *Acromastigum* has ventral stoloniform branches that are terminal in origin, replacing one half of an underleaf. This *Acromastigum*-type branching is found in other genera of hepatics, but does not occur in *Bazzania*. These branches occur, for example, in a few *Lepidozioideae* (e.g., *Lepidozia spinosissima*, *L. pumila* [Fig. 42: 3]), a few species of *Telaranea* and some *Zoopsidoideae* (*Paracromastigum*). In a number of *Acromastigum* species the stem cortex consists of a fixed number of 7 rows of cells that are larger than those of the medulla. The number of cortical cells may be as many as 16 (*A. cavifolium*, *A. colensoanum* and *A. verticale*) and the extreme reduction in number is reached in *A. rigidum* R.M.Schust. (Schuster, 1997b) of New Caledonia, in which the medulla is formed of only 3 cell rows. None of the species of *Bazzania* has a fixed number of stem cortical rows or has such extreme reduction in medullary cell number. Also, all New Zealand species of *Acromastigum* have either unlobed or bilobed leaves vs. tridentate or 3-lobulate leaves in all of the New Zealand representatives of *Bazzania*. In general, *Acromastigum* species are much smaller and more rigid than species of *Bazzania*.

References: Engel and Merrill (1994); Hodgson (1954; rev.); Schuster (2000a).

Key to Species

1a. Underleaves undivided; leaves transversely inserted, undivided or the apex short-bidentate. Sect. *Acromastigum* 2
  2a. Leaves triangular, with a strongly widened base and narrow apex, the apex at times retuse or shallowly and equally or unequally 2–3-fid; leaf cells distinctly larger in median-basal sector, forming a subvitta . . . . . *A. verticale* (p. 395)
  2b. Leaves subsymmetrically narrowly ovate, without a strongly widened base and with apex broader, rounded to truncate, undivided; leaf cells ± uniform throughout, without differentiation of a subvitta. Leaves transversely inserted and oriented, squarrose at least in basal half . . . . . *A. cavifolium* (p. 392)

1b. Underleaves 3-lobed or 3-toothed; leaves incubously inserted, 2-lobed or 2-toothed. Sect. *Inequilaterae* 3
  3a. Plants with secondary pigments, the leaves golden to brown, the stems darker, red-brown to blackish 4
    4a. Leaves small in proportion to stem; vitta ill-defined; leaf lobes reduced, the

dorsal reduced to a mere short, lateral projection 2–4 cells long; leaves with scattered bistratose areas . . . . . *A. brachyphyllum* (p. 413)

4b. Leaves large in proportion to stem; vitta distinct, in ventral sector of leaf; leaf lobes well developed and distinct, the dorsal lobe conspicuous and well defined; leaves unistratose throughout 5

5a. Vitta extending along the ventral side of leaf, or separated from it by 1 row of only slightly smaller cells, extending into the ventral lobe of the leaf; ventral lobe of leaf as much as 4× longer than the dorsal, 3–4 cells wide at base but biseriate for much of its length (including several biseriate tiers in basal half of lobe); leaves often strongly deflexed and then the ventral lobes of opposing leaves approximate in ventral aspect . . . . . *A. mooreanum* (p. 409)

5b. Vitta separated from ventral margin by 2–3 rows of small, ± isodiametric cells; ventral lobe of leaf typically less than twice the dorsal lobe in length, 4–6 cells wide at base, gradually narrowing to the tip (biseriate tiers, if present, only toward lobe apex and lacking in basal half of lobe); leaves moderately deflexed, the ventral lobes of opposing leaves never approximated . . . . . *A. anisostomum* (p. 407)

3b. Plants green or clear yellowish green, without brownish or reddish pigments 6

6a. Leaves subsymmetrically lobed, the lobes about equal in width and length, or the ventral lobe somewhat narrower; underleaves small, quadrate, often distinctly narrower than the conspicuously fleshy stem; stem cortex of more than 7 cells. Common species . . . . . *A. colensoanum* (p. 398)

6b. Leaves unequally lobed, the ventral lobe much narrower than the dorsal, or reduced to a tooth or crenulation; underleaves larger, wider than the stem; stem cortex of 7 cells. Rare species 7

7a. Dorsal lobe of leaf about equal to the ventral lobe in length, but the ventral lobe linear and biseriate to the base; cells in dorsal sector of leaf middle 19–29 μm wide and long, firm and moderately thick-walled; leaves with a ± distinct vitta along ventral margin; surface smooth or at most the lobes somewhat papillose . . . . . *A. cunninghamii* (p. 402)

7b. Dorsal lobe mostly reduced to a tooth or a crenulation, much smaller than the ventral lobe; cells (outside vitta in ± median sector of leaf) 12–14 μm wide and long; leaf cells strongly incrassate; leaves with a subvitta of 2–3 rows of larger cells in median-basal sector; surface coarsely papillose throughout . . . . . *A. marginatum* (p. 405)

Acromastigum cavifolium R.M.Schust.

Acromastigum cavifolium R.M.Schust., J. Hattori Bot. Lab. 26: 257. 1963. Type: New Zealand, Stewart Is., Tin Ra., *Schuster 53119.*

Plants appearing radially symmetric, rigid and appearing stout and fleshy, rather fragile, loosely prostrate, translucent, pure light green in life, pale straw-yellow in herb., distinctly nitid when dry; shoots small, to 1 mm wide. Branching of *Frullania* type, widely spreading;

branch half-leaf similar to leaves but somewhat narrower at apex, symmetric, ovate, undivided, tapering to a narrow apex; first branch underleaf undivided, lingulate, faintly sulcate, inserted on ventral side of main axis well below branch and closely juxtaposed on one side to a leaf, but not connate with it, or inserted on the ventral side of branch just above the juncture of branch and main shoot. *Acromastigum*-type branches common, stoloniform, the half-underleaf resembling the first branch underleaf of *Frullania*-type branches. Ventral-intercalary branches rare, leafy. Stem with cortical cells moderately differentiated, in 14–16 rows, thick-walled (particularly the outer tangential wall), moderately larger than the distinctly thick-walled medullary cells. Leaves rigid, appearing thick and fleshy, vertical or nearly so, not or at most feebly elevated, squarrose at least in basal half, the distal sector becoming gently suberect; leaves distant to loosely imbricate, plane to slightly and broadly concave, not vittate, 320–475(640) μm wide × 430–640 μm long, transversely inserted and oriented, subsymmetrically narrowly ovate, with a glistening border formed by the strongly thickened free walls of the marginal cells; apex undivided, narrowly to broadly rounded to broadly obtuse (rarely retuse); dorsal and ventral margins similar although the dorsal at times ± ampliate, the margins straight distally, weakly cordate at the base, entire. Cells in ± regular longitudinal rows at least in median sector, highly uniform almost throughout the leaf, moderately thick-walled, trigones massive, coarse and nodular, at times confluent, commonly with leaf cell lumen bounded mostly by the massive trigones (except for the narrow, moderately thick-walled places between trigones); subapical cells 20–30 μm wide and long, the median cells remaining ± isodiametric, being 22–34 μm wide and long, the basal cells to 36 μm long; surface smooth, papillose at the margins. Oil-bodies (*fide* Schuster, 2000a) 1–2(3) per cell, finely granular-botryoidal, colorless to greyish, spherical and 4.5–5(6) μm in diam. to ovoid and 4.5–5.5 × 6–8 μm. Underleaves with orientation and shape ± similar to the leaves but smaller, somewhat broader than the stem, distant to weakly imbricate, slightly convex; apex undivided, rounded and entire or retuse or very shallowly and often asymmetrically bifid, with 3 slime papillae in the apical notch; margins entire; cells as in leaves; surface smooth.

Androecia hyaline, on short, determinate, tightly spicate, ventral-intercalary branches from main shoot, or from leading, leafy ventral-intercalary branches or (often) from stoloniform branches; bracts ventricose-cucullate, the apex with 2 small, closely approximate teeth; dorsal and ventral margins similar, entire and lacking slime papillae; antheridia 1 per bract, the stalk biseriate; bracteolar antheridia occasional, 2 per bract. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem. Bracts of innermost series much larger than leaves but relatively small in proportion to perianth size, erect and closely appressed to perianth, the bracts concave-subcanaliculate, ovate, 4-lobulate, the median pair of lobes larger; lobes consisting of a few biseriate tiers from a base at most 4 cells wide, the lobe terminating in 2 laterally juxtaposed cells, a single cell or a uniseriate row of at most 2 cells, with each lobe terminating in a slime papilla; lamina in distal sector comprised of thick-walled cells with bulging trigones, the cells in basal portion thin-walled and with trigones minute or absent, the margins irregularly crenulate by the projecting, truncate, upper ends of some cells which each terminate in a slime papilla; bracteole similar in size and form. Perianth prominent, fusiform, terete below, trigonous above, plicate in distal ca. 0.25 and gradually narrowing to the contracted mouth, the mouth lobulate, the lobules each with 1- or 2-spinose, often contorted teeth composed of thick-walled cells, the teeth of a few laterally juxtaposed cells or, more often, comprised of a single cell or a uniseriate row of 2–3 cells.

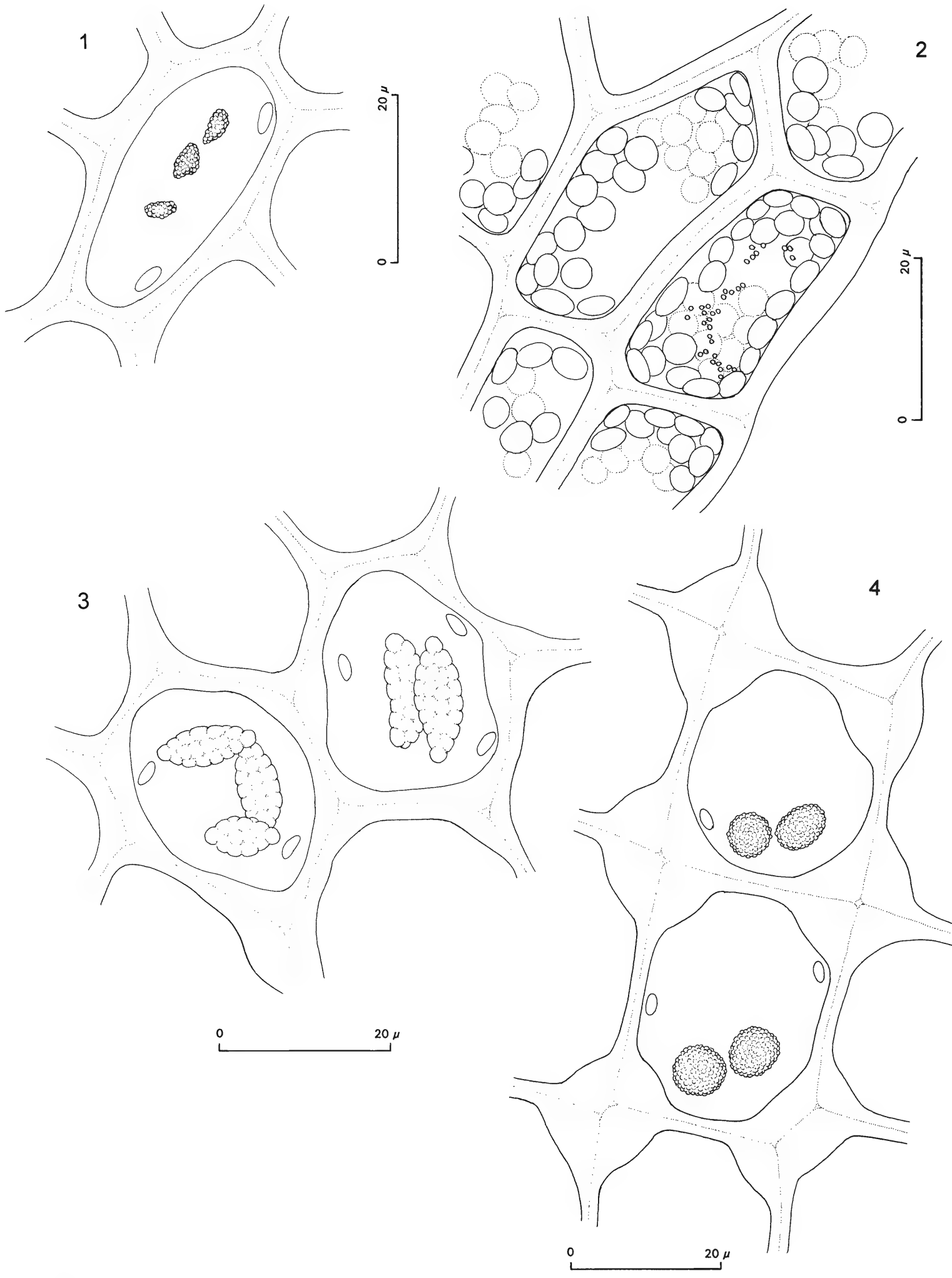

Fig. 85.
1. *Kurzia compacta* (Steph.) Grolle. Oil-bodies from cell of lower part of lobe, the outline of a few chloroplasts included. 2. *Drucella integristipula* (Steph.) E.A.Hodgs. Cells of lobe base showing tiny lipid droplets and notably large chloroplasts. 3. *Acromastigum brachyphyllum* A.Evans. Vitta cells, the outline of a few chloroplasts included. 4. *Acromastigum verticale* (Steph.) E.A.Hodgs. Cells of leaf middle, the outline of a few chloroplasts included. (Fig. 1, from *Glenny 9106*, New Zealand, South Is., Westland EP, Mt. Brown; 2, from *Glenny 9261*, New Zealand, South Is., West-

Seta seen only in collapsed state. Capsule wall 32–36 μm thick, of 3 layers, the outer layer about equal to thickness of the other 2 layers or a little more; outer layer of cells short-rectangular, with two-phase development, the longitudinal walls with rather thick, nonsinuous, sheet-like thickenings and strong nodule-like thickenings alternating with walls that are devoid of thickenings, the transverse walls devoid of thickenings; innermost layer of cells narrowly long-rectangular, with semiannular bands, the bands usually complete.

Spores 15.4–19.7 μm in diam., deep red-brown, with rather distantly spaced, sharply defined papillae and short, wide vermiculate markings. Elaters not seen.

Distribution and Ecology: New Zealand: Stewart Island, South Island (0–1160 m), North Island (890 m); Australia: Tasmania. In New Zealand known from Fiordland (Henry Pass, Secretary Island), Westland (Jackson Bay, Paparoa Ra., ridge behind Westport, Stockton and Denniston plateaus) and Auckland (Mt. Moehau) EPs.

This species is infrequent and occurs scattered with other taxa or, less often, in ± pure but not dense mats. It may occur on stumps and peaty humus, or on tree bases, mixed with *Acromastigum anisostomum*, *Adelanthus falcatus*, *Bazzania involuta*, *Cuspidatula monodon*, *Herbertus oldfieldianus*, *Heteroscyphus decipiens*, *Hymenophyllum armstrongii*, *Lepicolea scolopendra*, *Radula dentifolia*, *R. scariosa* and *Riccardia crassa*, or bryophyte-covered tree bark (recorded on trunks of *Lagarostrobos colensoi*, *Libocedrus bidwillii*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides* and *Phyllocladus alpinus*) and then associated with *Acrochila biserialis*, *Goebeliella cornigera*, *Heteroscyphus menziesii*, *Lepicolea scolopendra*, *Paraschistochila tuloides* and *Riccardia furtiva*. The species is apparently confined to organic substrates in hyperhumid areas.

Comments: This is the species described by Hodgson (1954, p. 18) as *Acromastigum integrifolium* (Austin) A.Evans, a species which is now known to be restricted to the Hawaiian Islands. Schuster (1963a) listed several differences between *A. cavifolium* and *A. integrifolium* (as well as *A. verticale* of New Zealand), namely the strongly concave, spoon-shaped leaves (which are spreading but never squarrose) and the rounded leaf apices, which are only rarely retuse and never emarginate. The majority of the leaves are so concave that, when flattened under the cover glass, they tear. Distinctive is the very regular, almost unvarying leaf shape, with all leaves widest near the base and thus ovate-triangular in shape.

Of the New Zealand species of the genus, *Acromastigum cavifolium* can be confused only with *A. verticale*, but has basically symmetrically ovate leaves, often with blunt or narrowly truncate apices; it also has somewhat smaller cells, 20–30 μm wide and long in the subapical region.

Acromastigum verticale (Steph.) E.A.Hodgs.

[Fig. 85: 4, oil-bodies, p. 394; Fig. 86]

Bazzania verticalis Steph., Hedwigia 32: 214. 1893. *Mastigobryum verticale* (Steph.) Steph., Sp. Hepat. 3: 449. 1908. *Acromastigum verticale* (Steph.) E.A.Hodgs., Trans. Roy. Soc. New Zealand 82: 18. 1954. Type: New Zealand, "*leg.* Prof. Kirk inter No. 373" (G!).

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ern Nelson EP, Pupu walkway; 3, from *Glenny 9348*, New Zealand, South Is., Western Nelson EP, Mt. Augustus; 4, from *Glenny 9341*, New Zealand, Stewart Is., Blaikies Hill.)

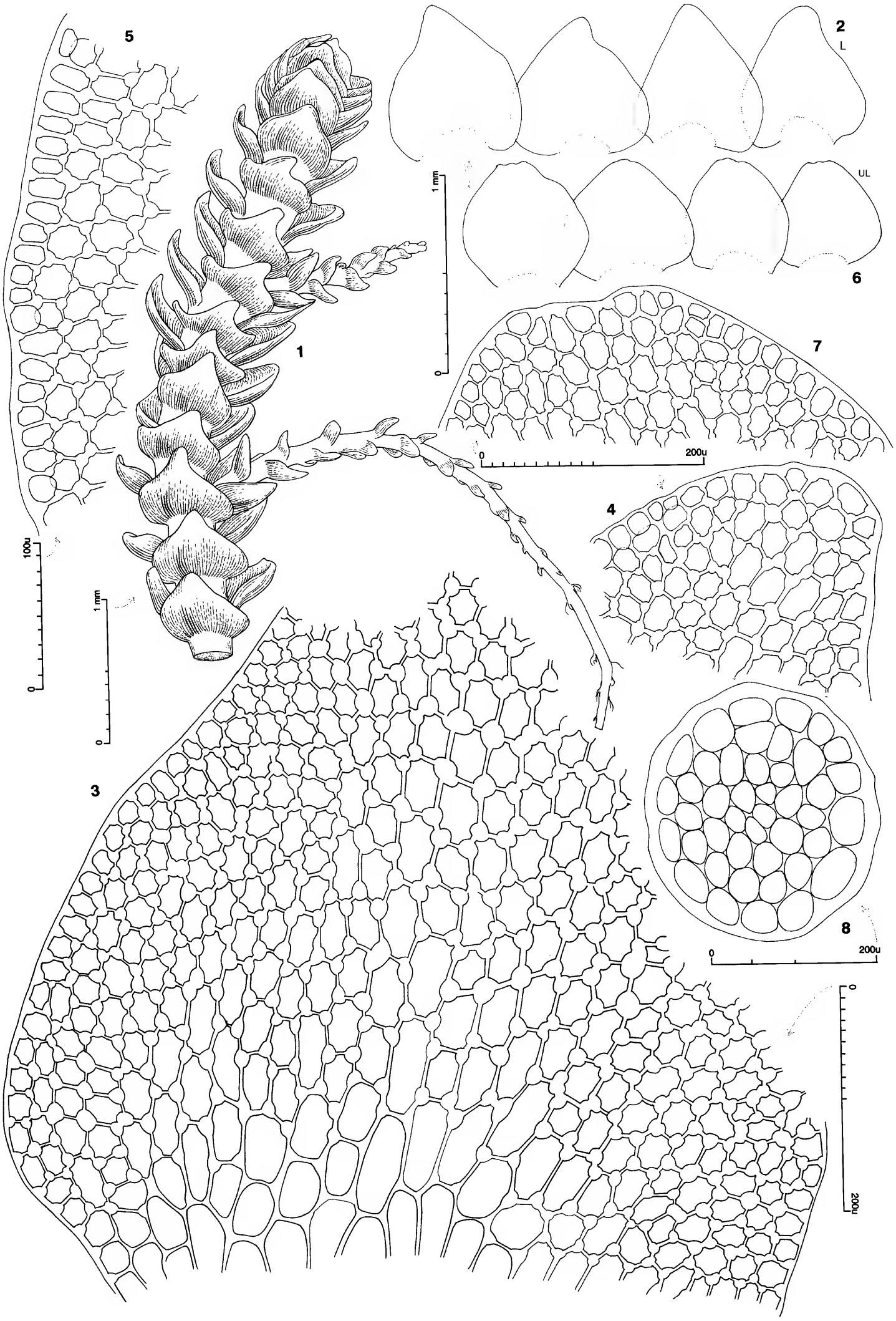

Fig. 86.
Acromastigum verticale (Steph.) E.A.Hodgs. 1. Portion of leading shoot with 2 *Acromastigum*-type branches, lateral view. 2. Leaves (= L). 3. Leaf, cellular detail. 4. Distal sector of leaf. 5. Portion of dorsal margin of leaf. 6. Underleaves (= UL). 7. Distal sector of underleaf. 8. Stem, cross section. (All from *Schuster*, *Scott* & *Taylor*, New Zealand, Stewart Is., Tin Ra. [*Hodgson 12026*, MPN].)

Acromastigum martinii E.A.Hodgs. *in* W.Martin, Trans. Roy. Soc. New Zealand 78: 496, 499. 1950, *nom. nud.*

Plants weakly anisophyllous, ± isophyllous in less robust sectors (common) of shoot, suberect, rigid, appearing fleshy, light green, nitid when dry; shoots small, to 1.2 mm wide. Branching infrequent, regularly of *Frullania* type; branch half-leaf ± symmetric, ovate, undivided, nonvittate, tapering to a narrow apex; first branch underleaf undivided, broadly ovate, inserted on ventral-lateral side of juncture of main axis and branch. *Acromastigum*-type branches common, stoloniform, rather short, the half-underleaf resembling the half-leaf of a *Frullania*-type branch. Stem cortical cells moderately differentiated, in 12–16 rows, the outer tangential wall thick-walled, the radial walls thin or slightly thickened, the cortical cells moderately larger than the slightly to moderately thick-walled medullary cells. Leaves rigid, vertical or nearly so, not dorsally assurgent, squarrose at least at base, with the narrowed distal sector of the leaf erect or hooked at the tip, approximate to loosely imbricate, moderately concave; leaves subvittate, 595–700 μm wide × 560–665 μm long, transversely to feebly incubously inserted and oriented; leaves variable in shape, somewhat asymmetrically triangular-ovate, with a broad base, acuminate, the apex narrowly acute, undivided or at times retuse or shallowly and equally or unequally 2(3)-fid (if 3-fid, the dorsal-most tooth at times displaced on dorsal margin and lower); margins entire, a pellucid border lacking, the dorsal margin ampliate and broadly cordate at the base, the ventral somewhat less so. Cells of leaf moderately thick-walled, with massive, nodular, knot-like trigones, the subapical cells 23–28 μm wide × 25–35 μm long, the median-basal cells much larger and elongate-rectangular, forming a broad subvitta, the subvitta cells 29–34 μm wide × 41–55 μm long, uniformly thick-walled, with less distinct trigones, the subvitta somewhat ventrally displaced; cells of the ampliate lateral and basal sectors ± isodiametric; marginal row of cells in lower half of leaf forming an indistinct border, the cells ± transversely elongate, their free walls strongly thickened; surface smooth throughout. Oil-bodies occupying a small portion of cell lumen, hyaline and somewhat glistening, with a milky appearance, (1)2 per median leaf cell, subglobose to broadly elliptic, finely and somewhat obscurely papillose, the spherules slightly protruding beyond membrane. Underleaves undivided, about as wide as stem or slightly wider, somewhat smaller than the leaves, ± subsymmetrically ovate (sometimes broadly so and then suborbicular), subvittate (but less so than leaves), the apex irregularly truncate or feebly notched at insertion of the 3 slime papillae; cells as in leaves; margins entire; surface smooth.

Capsule (*fide* Grolle, 1964h) with wall 3-stratose; outer wall with two-phase development, the longitudinal walls with sheet-like thickenings and distinct knot-like thickenings alternating with walls that are devoid of thickenings, the transverse walls devoid of thickenings or sporadically with an isolated nodule; innermost layer of cells narrowly rectangular, with 2–3 usually complete semiannular bands per cell.

Distribution and Ecology: New Zealand: Stewart Island (500 m), South Island (700 m), North Island, from only a few sites; Australia: Tasmania. On Stewart Island it occurs on moist, sandy soil at the head of Crooked Reach, Port Pegasus (*leg. Martin*) and from a creek bed (also Port Pegasus, *leg. Scott*); also known from the Tin Ra. in a penalpine meadow (*leg. Schuster, Scott & Taylor*, MPN) and from the walls of an incised stream (N of Mt. Allen, 500 m). On Stockton Plateau at 700 m, where it formed pure cushions of erect stems 10 cm deep in shallow water on an open streambed with sandstone bedrock and gravel bottom, surrounded by low *Leptospermum scoparium* scrub; accompanying species were *Adelanthus falcatus*,

Blindia robusta, *Cheilolejeunea* aff. *mimosa*, *Isotachis montana*, *Pachyglossa tenacifolia*, *Riccardia australis* and *Stigonema* sp. (a cyanobacterium). The type is from Great Barrier Island.

Comments: Distinct from other New Zealand species of the genus in the subvittate, triangular-ovate leaves and the abruptly narrowed, erect to inflexed leaf apices. In addition, the characteristic pellucid leaf margin, seen in varying degrees in all other New Zealand *Acromastigum* species is lacking in *A. verticale*. The only species likely to be confused with *A. verticale* is *A. cavifolium*, but this species has ± homogeneous areolation and more narrowly ovate leaves, with a broadly rounded to truncate apex. Also, the stem of *A. verticale* has a somewhat fleshy appearance, with a cortex of short, isodiametric, rather thin-walled cells as seen in surface view. For additional distinctions, see under *A. cavifolium*.

Acromastigum colensoanum (Mitt.) A.Evans

[Fig. 87; Fig. 90: 1, 2, oil-bodies, p. 410]

Mastigobryum colensoanum Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 147. *pl. 100, f. 3*. 1854. *Bazzania colensoana* (Mitt.) Carrington & Pearson, Pap. & Proc. Roy. Soc. Tasmania 1887: 50. 1888 ("*colensoii*"). *Acromastigum colensoanum* (Mitt.) A.Evans *in* Reimers, Hedwigia 73: 142. 1933. Type: New Zealand, North Is., Tararua, *Colenso*.

Mastigobryum minutulum Colenso, Trans. & Proc. New Zealand Inst. 19: 288. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso 1403* (BM!, G!).

Mastigobryum amoenum Colenso, Trans & Proc. New Zealand Inst. 19: 288. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso*.

Mastigobryum smaragdinum Colenso, Trans. & Proc. New Zealand Inst. 21: 67. 1889 (1888). Type: New Zealand, Waipawa Co., S of Dannevirke, 1888, *Colenso* (BM!).

Mastigobryum erosifolium Steph. *in* Steph. & Watts, J. Proc. Roy. Soc. N. S. W. 48: 122. 1914. Type: Australia, Cambewarra Mt., Oct. 1907, *Watts 917 – c. per.* (G!).

Plants delicate, soft and flexuous, grass-green to yellow-green, rarely bluish green, without secondary pigments, nitid when dry; shoots medium, to 1.8 mm wide. Branching pseudodichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf weakly asymmetric to ± symmetric, ovate, undivided, tapering to a narrowly rounded to sharply acute apex; first branch underleaf 2-lobed, inserted on ventral or ventral-lateral side of branch near the juncture of branch and main shoot. *Acromastigum*-type branches common, stoloniform. Ventral-intercalary branches sporadically produced, leafy. Stem fleshy in appearance, the cortical cells moderately differentiated, variable in number, somewhat larger than the medullary cells, in 14–16(18) rows, the radial walls thin like the medullary cells, the outer tangential walls somewhat thickened; cortical cells in dorsal view of surface short (ca. 50–70 μm long), the ventral cortical cells similar. Leaves typically persistent, exceptionally caducous, delicate, loosely imbricate, exposing much of stem in dorsal aspect, widely spreading, plane or slightly convex; leaves subvittate or not, asymmetrically narrowly ovate-rectangular, 360–530 μm wide × 730–900 μm long, the insertion strongly incubous, ± equally bilobed to 0.25–0.4, the ventral lobe often somewhat narrower and at times longer than the dorsal, the lobes acute, the dorsal often broadly so, the lobes at times apiculate, usually terminating in a single cell or sporadically in a uniseriate row of 2 cells, the dorsal lobe 7–12 cells wide at base, the ventral 5–7(8) cells wide; dorsal margin ± straight, cordate to subauriculate at base, extending to middle of stem or somewhat beyond, the ventral margin nearly straight, the margins

of disc and lobes entire or somewhat sinuate. Cells of leaf thin-walled and with minute trigones or evenly thick-walled and with medium and straight-sided trigones, with a short indistinct vitta (apparent only on some leaves) consisting of several rows of somewhat larger, somewhat elongated cells (24–34 μm wide × 26–36 μm long) in the ventral sector of leaf near the base and separated from the margin by 1–3 rows of cells, the cells of the dorsal sector of the leaf smaller, less regularly arranged, 14–23 μm wide × 17–28 μm long; marginal cells of disc and lobes with outer walls somewhat thickened; surface smooth or finely but distinctly papillose, near the base striate-papillose. Oil-bodies restricted to basiscopic half of leaf and in all vitta cells, but some cells (especially those in basiscopic lobe) lacking them, the oil-bodies completely lacking in acroscopic half of leaf with no traces of droplets there, the oil-bodies in vitta very variable, (2)6–12 per cell, very pale grey, elliptic to linear, smooth but organized into large, irregular, subspherical masses of oil with segmentation lacking, or, if present, obscure and mostly appearing to be a surface feature, the oil-bodies appearing irregularly lumpy, 4–7 × 9–11.6 μm; oil-bodies in nonvittate cells along basiscopic margin, 2–6 per cell; oil-bodies in cells of leaf base smoother, less lumpy and more *Bazzania*-like in appearance. Chloroplasts packed in nonvittate cells. Underleaves small, often narrower than stem (particularly on larger diameter stems), appressed to the stem or slightly spreading, distant, quadrate to rectangular, 3-lobed to 0.6; lobes ligulate, 2–4 cells wide at base, the apex truncate (often retuse) to rounded to bluntly acute, entire, terminating in 2–4 laterally juxtaposed cells or, less commonly, in a single cell; disc margins ± straight to somewhat curved, with entire margins; cells of disc and lobes thin-walled, the outer tangential wall of marginal cells thickened; surface smooth.

Androecia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from leading shoots; bracts ventricose-cucullate, ± symmetrically bifid to ca. 0.3, the lobes broad acute, often apiculate, terminating in a uniseriate row of 2 cells; dorsal margin not perceptibly dilated, sparingly repand, at times crenulate, with a few slime papillae, otherwise entire; bracts monandrous; antheridial stalk biseriate; bracteolar antheridia absent. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the gynoecium base slightly swollen and rhizoidous. Bracts of innermost series much larger than leaves, erect and closely ensheathing the perianth, the bracts concave-subcanaliculate, narrowly ovate, bilobed to ca. 0.3; lobes narrowly attenuate to linear, terminating in a uniseriate row of 2–3 cells, the lobe margins subentire or with a few remote crenulations; lamina composed of subrectangular, thin-walled cells, the marginal and submarginal cells ± rhomboidal, variable in shape, minutely and irregularly crenulate by projecting ends of cells, the margin on each side with an indistinct lobule in upper third; bracteole similar in size and form. Perianth prominent, straight, fusiform, terete below, the distal 0.75 pluriplicate and gradually narrowing to the contracted mouth, the mouth with 6 narrowly attenuate, somewhat sinuous lobes that each terminate in a uniseriate row of 2–3 cells, the lobe margins irregularly serrulate and at times with a few accessory teeth and laciniae; perianth 2-stratose in basal sector.

Seta with 8 rows of very large outer cells, the interior cells not seen. Capsule wall 42–45 μm thick, of 2 subequally thick layers; outer layer of cells subquadrate, with two-phase development, the longitudinal walls with rather thin, nonsinuous, sheet-like thickenings and several nodule-like to spine-like thickenings alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells ± tiered, mostly quadrate to occasionally short-rectangular, with semiannular bands 1–2 per cell, the bands frequently semicircular at the cell corners,

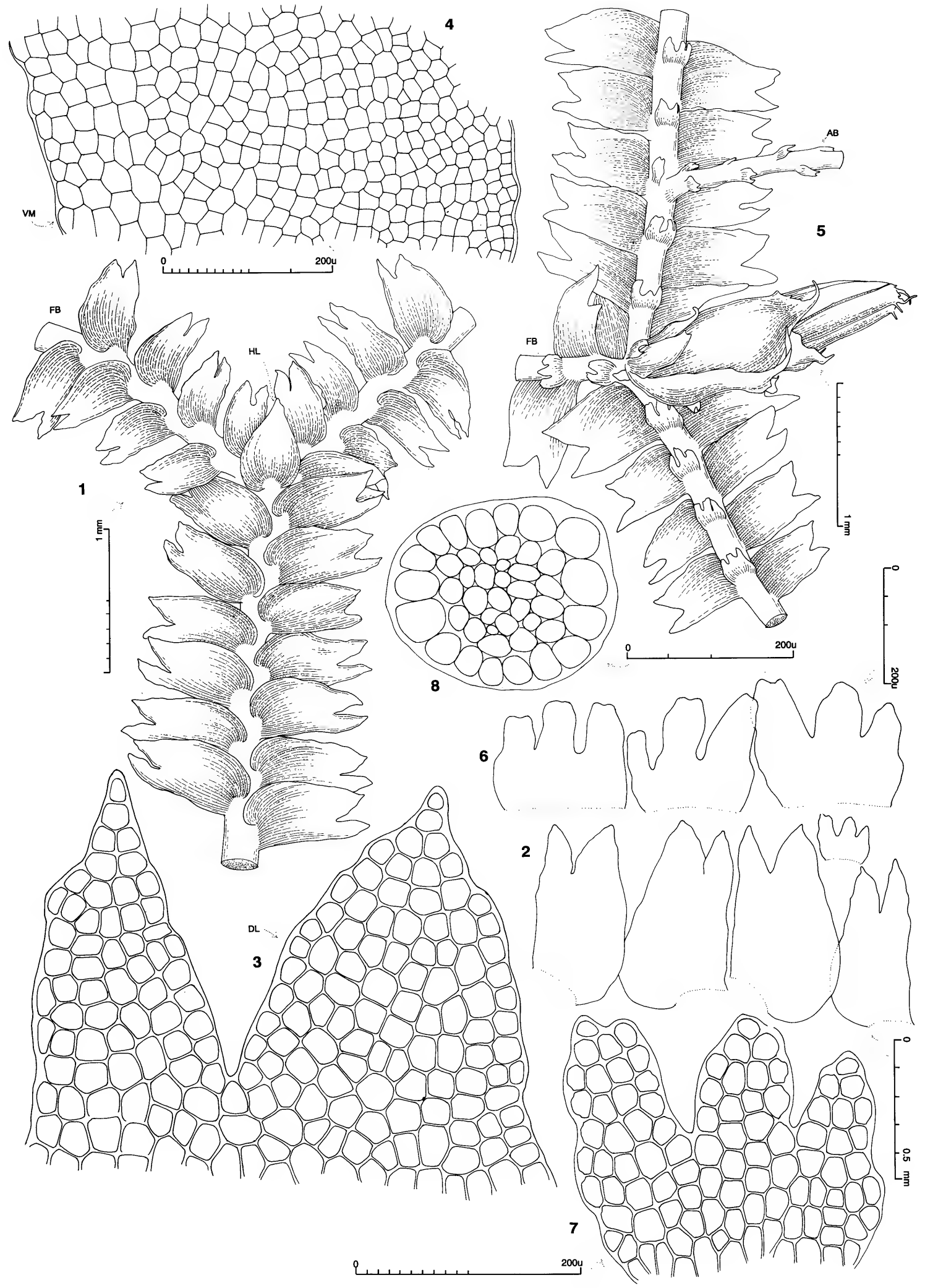

Fig. 87.
Acromastigum colensoanum (Mitt.) A.Evans. 1. Portion of leading shoot with *Frullania*-type branch (= FB), dorsal view (HL = half-leaf). 2. Leaves and above, underleaf at same scale. 3. Distal sector of leaf (DL = dorsal lobe). 4. Basal portion of leaf with weak differentiation of a vitta (VM = ventral margin). 5. Portion of leading shoot with perianth and *Frullania*-type branch (= FB,

rather wide, usually complete, rather frequently forked and anastomosing to delimit ill-defined, local fenestrae; tangentially oriented bands occasional (seen in capsule cross section).

Spores and elaters not seen.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island (530 m), South Island (100–600 m), North Island (420–1100 m), Chatham Islands; Australia: Tasmania, New South Wales. Known from Fiordland, Otago, Westland, Sounds–Nelson, Southern North Island, Volcanic Plateau, Taranaki, Gisborne, Auckland and Northland EPs.

A relatively common species of wet forests. It occurs on bryophyte-covered logs, rotted stumps, tree buttresses (particularly in protected recesses between exposed roots at the tree base) and occasionally on tree-fern caudices. It also is found loosely creeping over soil deep in shaded, protected hollows or pockets, at times with *Telaranea elegans* and *Saccogynidium australe*, and it may form loose, soft mats on cliff faces. Also over soil on vertical mossy banks or mossy stream banks. In the Herangi Ra. (vicinity of plateau area S of Te Whakapatiki, ca. 720–750 m) over humus in a very narrow and shallow water channel in a small valley system, the vegetation consisting of *Podocarpus hallii*, *Dracophyllum traversii* and *Weinmannia* to 3–5 m tall. On Stewart Island it occurs deep in shaded, protected niches under tussock cover within mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus* (Mt. Rocky summit area, 530 m). Commonly accompanying species are *Bazzania nitida*, *Leucobryum candidum*, *Rhizogonium distichum* and *Zoopsis argentea*. Also found with *Bazzania adnexa*, *Cuspidatula monodon*, *Psiloclada clandestina*, *Pyrrhobryum bifarium*, *Rhynchostegium tenuifolium*, *Saccogynidium australe*, *Trichocolea mollissima*, *Tylimanthus diversifolius*, *Wijkia extenuata*, *Zoopsis argentea* and *Z. setulosa*. The habitats of this species seem to be more nutrient-rich and less constantly moist than those of other *Acromastigum* species, as indicated by some of the species that can be found with *A. colensoanum*.

Comments: This species is easy to recognize because of its grass-green color (secondary pigments totally absent) and the nonvittate, subsymmetrically lobed leaves, with the two lobes about equal in size and width (Fig. 87: 1, 2). The stems appear stout and fleshy, due to the stem cortex of more than 7 cell rows (Fig. 87: 8). This species is the only one in the genus here that is commonly seen with sporophytes.

The inner capsule wall occasionally has tangentially oriented bands; these are seen in capsule cross section and are oriented at right angles to the vertical bands that are so common in the Hepaticae. We know of no other instance of such tangential bands.

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note bifid first branch underleaf) and *Acromastigum*-type branch (= AB, note half-underleaf), ventral view. 6. Underleaves. 7. Underleaf, cellular detail. 8. Stem cross section. (Figs. 1–7, from *Engel 19192*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., S side of Pororari R.; 8, from *Hatcher 934*, New Zealand, South Is., Westland EP, Martins Bay.)

Acromastigum cunninghamii (Steph.) A.Evans

[Fig. 88]

Bazzania cunninghamii Steph., Hedwigia 32: 205. 1893. *Mastigobryum cunninghamii* (Steph.) Steph., Sp. Hepat. 3: 540. 1909. *Acromastigum cunninghamii* (Steph.) A.Evans, Ann. Bryol. Suppl. 3: 106. 1934. Lectotype (cf. Fulford, 1966): Chile, Prov. Magellanes, Puerto Gray, *Cunningham 147* (BM, *non vidi*).

Plants loosely prostrate or erect and cushion-forming, typically bright pale yellowish green, rarely pure green or bluish green, distinctly nitid when dry; shoots small, to 1 mm wide. Branching pseudo-dichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf ± symmetric, narrowly ovate, undivided, subvittate, tapering to a sharp apex; first branch underleaf 2–3-lobed, similar in form to other underleaves, inserted on ventral or ventral-lateral side of branch, quite removed from branch base. *Acromastigum*-type branches common, stoloniform. Stem cortical cells distinctly differentiated, in 7 rows, moderately thick-walled (the outer tangential wall thicker), distinctly larger than the thin-walled medullary cells; cortical cells in dorsal view of surface very large (100–130 μm long), hexagonal, the ventral cortical cells ± quadrate, about half as large and at times broader than long. Leaves typically persistent, rarely caducous, horizontal, loosely imbricate, allowing little of stem exposed in dorsal aspect, obliquely spreading, the dorsal portion plane, the ventral ± convex, the apex somewhat deflexed (particularly the ventral lobe); leaves indistinctly vittate, asymmetrically narrowly ovate, 220–330 μm wide × 480–770 μm long, the insertion strongly incubous; apex ± equally bilobed to 0.3–0.4, the ventral lobe slightly longer or about equal in length to the dorsal but distinctly narrower, the lobes entire, terminating in a single cell or uniseriate row of 2 cells; dorsal lobe narrowly acute, 4–6 cells wide at base; ventral lobe linear, divergent to ± parallel with the dorsal (when flattened), biseriate for most of its length, 2(3) cells wide at the base; dorsal margin ± straight, cordate to subauriculate at base, extending to middle of stem or somewhat beyond, entire or somewhat sinuate; ventral margin nearly straight, entire. Cells of leaf evenly thick-walled, without distinct trigones, with 2 rows of larger, rectangular cells along the ventral margin of leaf and continuing into the ventral lobe, forming an indistinct vitta, the inner row often somewhat larger, the cells of vitta 20–30 μm wide × 24–37 μm long, the cells in the dorsal sector of leaf smaller, less regularly arranged, 19–29 μm wide and long; marginal cells of disc and lobes with outer walls thickened and forming a glistening border; surface smooth or the lobes ± distinctly papillose. Oil-bodies 1 per cell, colorless, homogeneous, the surface smooth, the oil-bodies spindle-shaped, 2 × 3–5 μm. Underleaves conspicuous, a little wider than the stem, erect and ± appressed to the stem, contiguous, moderately convex, orbicular to quadrate, 3-lobed to 0.35–0.65; lobes ligulate, 2–4 cells wide at base (the lobes subequal or the lateral lobes somewhat wider), the apex truncate to acute, entire, terminating in a single cell (or uniseriate row of 2 cells) or 2–4 laterally juxtaposed cells; disc margins ± straight to curved; cells of disc and lobes evenly thick-walled; disc margins entire; surface smooth or distinctly but finely papillose.

Androecia and gynoecia not seen.

Distribution and Ecology: Amphi-Pacific in distribution (Engel and Merrill, 1994): southern South America; New Zealand: Auckland Islands, Stewart Island (200 m), South Island (120–1200 m), North Island (60–1300 m). It is apparently sporadic but widespread in New Zealand and is known from Fiordland (Borland Burn, Lake McKerrow), Westland (Haast Pass), Western Nelson (Stockton Plateau, Mt. Glasgow), Gisborne (Urewera), Auckland (Herangi Ra., Kaimai Ra., Coromandel Peninsula) and Northland (Waipoua Forest) EPs.

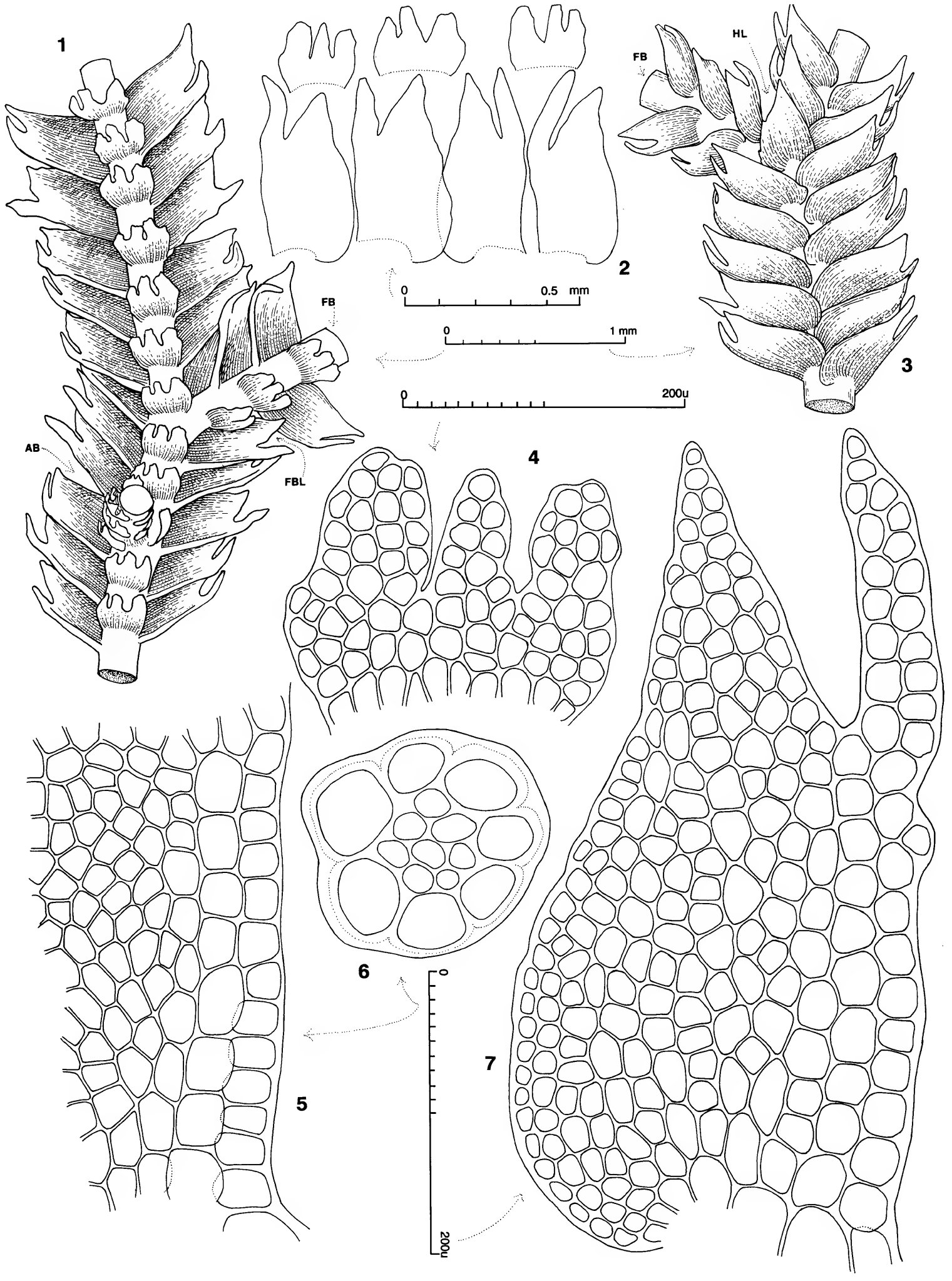

Fig. 88.
Acromastigum cunninghamii (Steph.) A.Evans. 1. Portion of leading shoot, with *Frullania*-type branch (= FB, FBL = first branch underleaf) and *Acromastigum*-type branch (= AB, at arrow, note half-underleaf), ventral view. 2. Leaves, and above, underleaves at same scale. 3. Portion of leading shoot; note FB (= *Frullania*-type branch) and its half-leaf (= HL), dorsal view. 4. Underleaf. 5. Ventral sector of leaf showing differentiation of a marginal vitta. 6. Stem, cross section. 7. Leaf. (All from *Hatcher 1452*, New Zealand, South Is., Westland EP, head of Lake McKerrow.)

Usually on rock, especially on the sides of boulders and on stones in periodically inundated streambeds, but also on rock walls exposed to water flow, and on humus in constantly damp places. On Stewart Island plants occurred in a protected pocket with *Acromastigum marginatum* at the base of a large rocky outcrop in a podocarp–hardwood forest including *Dacrydium cupressinum* and *Weinmannia racemosa* (Port Pegasus, vicinity of Tin Ra. Track, 200 m). An Auckland Island specimen was on tree branches in the direct spray from a waterfall. In the South Island it may occur directly on rock substrate of a huge boulder as well as dripping cliff faces in *Nothofagus menziesii* forest (Haast Pass, 540 m and Blue Valley Track, 430–480 m) where it may form large, spongy pure masses. In the North Island known from Urewera Natl. Park (crest trail from Highway 38 toward Whakataka summit, growing loosely in a deep recess at a tree base in a *Nothofagus fusca – N. menziesii* forest, 930–1030 m) and the summit area of Te Rangaakapua (Huiarau Ra., Urewera Natl. Park, 1230–1320 m) on a vertical rock wall in a mossy forest dominated by *N. menziesii* with some *Olearia colensoi*. Also present on the Herangi Ra. (vicinity of plateau area S of Te Whakapatiki, ca. 720–750 m), beneath decaying leaves of *Poa* sp. at the base of a vertical cliff. It occurs in the Kaimai Ra. (Aongatete area, 60 m) where plants occurred on a vertical rock wall at the margin of a stream system near several pools and low waterfalls where periodic inundation occurs, and on Mt. Te Aroha (880–940 m) occurring over rock and forming pendent sheets in a forest dominated by *N. menziesii*. On Coromandel Peninsula (ridge between Webb Creek Track and Billy Goat Track, Coromandel Forest Park, 510–540 m) on a shaded moist bank at a creek edge in a scrub forest of *Leptospermum scoparium*, *Weinmannia silvicola* and *Dacrydium cupressinum*; also on Mt. Moehau (ca. 800–840 m) on vertical banks of an exposed rocky ridge below the summit area of "Little Moehau" in an area of rocky outcrops and shrub-heath communities including *Coprosma foetidissima*, *Corokia buddleioides*, *Dracophyllum recurvum*, *Lepidothamnus laxifolius* and *Oreobolus pectinatus*. On Mt. Glasgow (Westland, 1200 m) it was found in a water course in penalpine shrub-tussockland of *Olearia colensoi*, *Chionochloa flavescens*, *C. pallens* and *C. australis*.

Comments: The narrow, biseriate ventral lobes of the leaf (Fig. 88: 7), the firm texture of the plants and clear straw-yellow color will immediately distinguish *Acromastigum cunninghamii* from the other bilobed-leaved New Zealand species of the genus. The common *A. colensoanum* also lacks secondary pigments, but differs by its subequally lobed leaves, lax texture, grass-green color and thicker stems (the cortical cells often in more than 7 rows).

The leaves of *Acromastigum cunninghamii* have a distinctive type of vitta, which is not intramarginal, but consists of 2 regular rows of larger quadrate cells along the ventral margin which extend distally to form the biseriate ventral lobe (Fig. 88: 7). The cell walls of the leaf are often suffused by a pale yellow pigment and are evenly thickened, except for the outer walls of the cells along the leaf margin, which are thicker (Fig. 88: 7) and form a narrow, glistening border.

Populations of *Acromastigum cunninghamii* from southern Chile differ by having more sinuate leaf margins and a coarsely papillose surface, but are otherwise similar to the New Zealand plants.

Acromastigum marginatum E.A.Hodgs.

[Fig. 89]

Acromastigum marginatum E.A.Hodgs., Trans. Roy. Soc. New Zealand 82: 22. *pl. 2, f. 10, 11.* 1954. Holotype: New Zealand, Great Barrier Is., Forestry Camp, 800 ft., 10 April 1952, *Lloyd 39* (MPN hb. Hodgson no. 8433, *non vidi*); isotype: (CHR!).

Plants rigid and wire-like, fragile, loosely creeping among other cryptogams, bright green when fresh, pale translucent yellow-green in herb., without secondary pigments, dull when dry; shoots small, 665–770 μm wide. Branching ± regularly pseudo-dichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf slightly asymmetrically ovate, undivided, nonvittate, tapering to a sharp apex, cordate at base; first branch underleaf 2-lobed, inserted on ventral-lateral side of juncture of main axis and branch, free and often distant from underleaf of main axis. *Acromastigum*-type branches common, stoloniform, rarely reverting to leafy. Stem cortical cells distinctly differentiated, in cross section in 7 rows, moderately thin-walled except for the strongly thickened outer wall (the ventral 2 rows much smaller), distinctly larger than the thin-walled medullary cells which are in 7–8 rows; cortical cells in dorsal view of surface very large, 46–53 μm wide × 84–96 μm long, ± hexagonal, the ventral cortical cells ± quadrate, 26–32 μm wide × 34–43 μm long. Leaves rigid, fragile, easily tearing, loosely imbricate, with little of stem exposed in dorsal aspect, widely spreading, plane to slightly convex, with a thickened, pellucid margin, subvittate, asymmetrically narrowly ovate, 210–240 μm wide × 315–355 μm long, the insertion moderately incubous; leaves shallowly and strongly asymmetrically bilobed to ca. 0.15–0.2, the ventral lobe much larger than the dorsal, the lobes entire, terminating in a single cell or 2 superposed cells, the dorsal lobe truncate or reduced to a tooth or crenulation, the ventral lobe acute, 4–5(6) cells wide at base; dorsal margin broadly and gently curved, cordate to subauriculate at base, extending to middle of stem or somewhat beyond, entire or somewhat sinuate, not decurrent; ventral margin straight or slightly curved distally, abruptly curved near the base, entire, not decurrent. Cells of leaf evenly very thick-walled, with a subvitta in the median-basal area somewhat nearer the ventral margin than the dorsal, separated from the ventral margin by 2–3 rows of cells; cells ± in longitudinal rows, those outside the vitta in median sector of leaf 12–14 μm wide and long (the vitta cells larger, 18–24 μm wide × 22–25 μm long); surface striate-papillose along the margins of leaves, the dorsal surface coarsely papillose, the ventral almost smooth, except at margins. Underleaves large, to 2× stem width, contiguous, oblate in outline, 3-lobed to ca. 0.5; lobes subattenuate, 4–7(11) cells wide at base (the lobes subequal or the lateral lobes somewhat wider), the apex obtuse to acute, entire, terminating in a single cell or more commonly 2–4 laterally juxtaposed cells; disc margins broadly and distinctly curved, dilated near base into a rounded or angular projection, then often auriculate; cells of disc and lobes evenly thick-walled; surface papillose.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand, where it has a broad but evidently sporadic distribution; present on Stewart Island (20–200 m), South Island (20–700 m), North Island (ca. 350 m). Known from Rakiura (Port Pegasus, Tin Ra.), Fiordland (Secretary Island, Lake Manapouri), Westland (Cascade Plateau, Mt. Te Kinga), Western Nelson (Denniston Plateau, Stockton Plateau, Marino Mtns., Pakawau), Volcanic Plateau (Kaimai Ra.), Auckland (Coromandel, Great Barrier Island) and Northland (Waipoua) EPs.

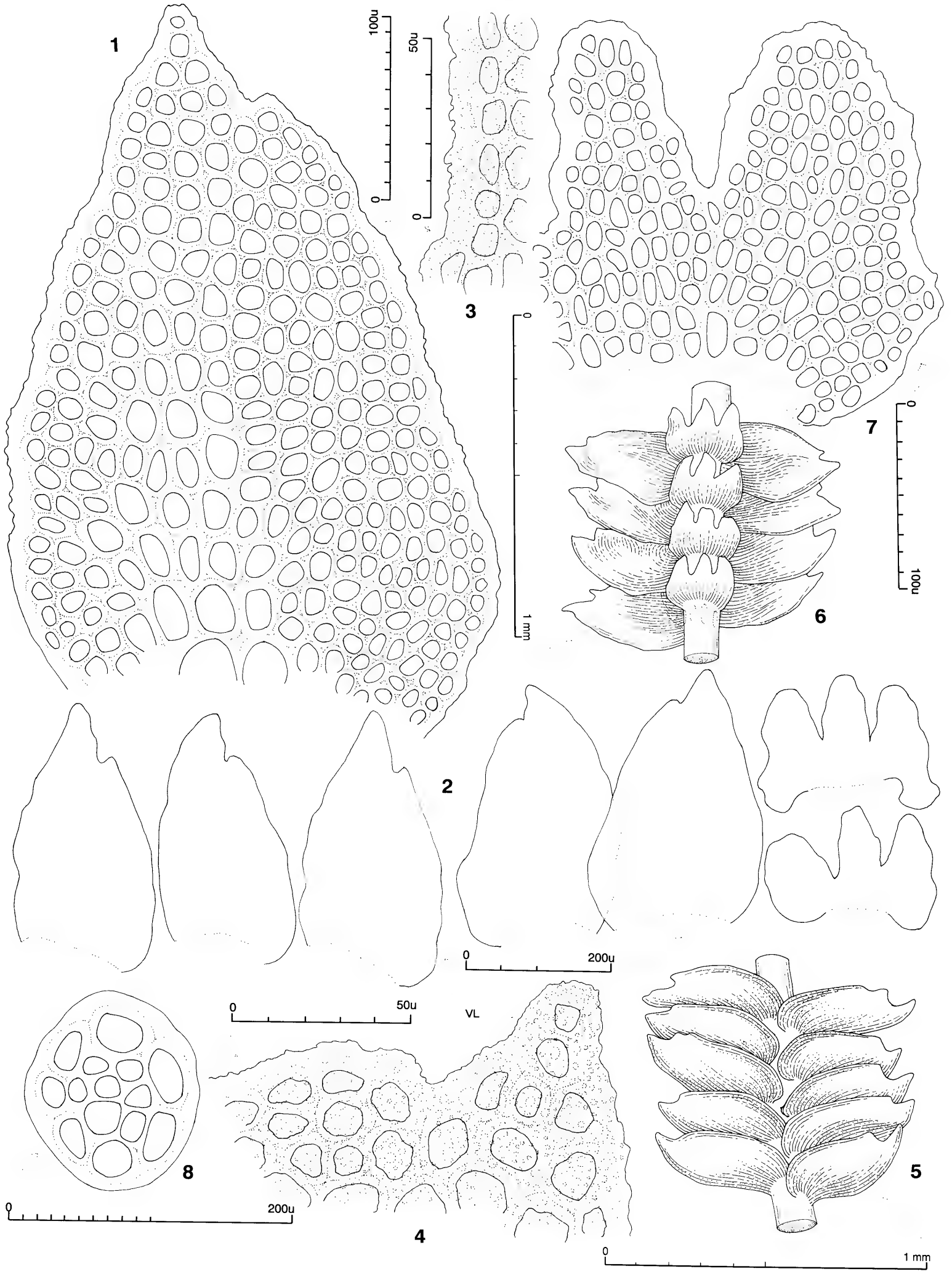

Fig. 89.
Acromastigum marginatum E.A.Hodgs. 1. Leaf, cellular detail. 2. Row of leaves and to right underleaves, at same scale. 3. Marginal cells of dorsal, ampliate sector of leaf. 4. Distal sector of leaf (VL = ventral lobe). 5. Sector of leading shoot, dorsal view. 6. Sector of leading shoot, ventral view. 7. Portion of underleaf, cellular detail. 8. Stem, cross section. (All from type.)

Usually under forest (including *Agathis australis – Beilschmiedia* forest, *Nothofagus menziesii* forest, *Dacrydium cupressinum – Weinmannia racemosa* forest) or low podocarp forest or scrub (*Lepidothamnus intermedius* or *Halocarpus bidwillii* scrub with *Leptospermum scoparium*). It is found on tree bases, rarely on tree trunks, on vertical or slightly overhanging rock walls protected from direct rainfall, and on forest floor humus. Associated species are *Acromastigum anisostomum*, *Bazzania monilinervis*, *B. nitida*, *Porina exocha*, *Hymenophyllum armstrongii*, *H. demissum*, *H. flabellatum*, *Kurzia hippuroides*, *Metrosideros diffusa*, *Paraschistochila conchophylla*, *Psiloclada clandestina*, *Ptychomnion aciculare*, *Riccardia crassa* and *Zoopsis argentea*.

On Stewart Island plants occurred with *Acromastigum cunninghamii* over soil deep in a protected pocket at the base of a large rocky outcrop in a podocarp–hardwood forest including *Dacrydium cupressinum* and *Weinmannia racemosa* (Port Pegasus, vicinity of Tin Ra. Track, 200 m). In the South Island known from 200 m on Secretary Island, Fiordland, and at 135 m in the Cascade ultramafic moraine (W of Martyr Saddle, SSW of Jackson Bay), an area of ultramafic rocks and outcrops with rather open vegetation consisting of mainly of *Gleichenia*, *Lycopodium*, *Juncus*, the lichen *Cladonia* and scattered *Leptospermum scoparium*. In the North Island on the Kaimai Ra. (Aongatete area, 60 m) where plants occurred on a vertical rock wall above a stream system near several pools and low waterfalls. Also known from the summit of Table Mtn. (Coromandel Forest Park, 835 m), on the side of a bryophyte-covered log as well as over bark at tree base in a wet mossy forest of *Lepidothamnus intermedius*, *Ixerba brexioides* and *Dacrydium cupressinum* with occasional *Phyllocladus glaucus*. In Waipoua Forest (track to Te Matua Ngahere, ca. 340 m) at the base of a huge *Agathis* tree in mixed *Agathis australis – Dacrydium cupressinum* forest with other podocarps and with a dense ground tier of *Gahnia xanthocarpa*. In more humid sites in Waipoua Forest found loosely in masses of vegetation of a vertical stream bank in a steep-sided stream valley (Waikohatu Stream, 290 m). In Omahuta Forest Kauri Sanctuary (E of Mangamuka Bridge, Northland, 260 m) on bryophyte-covered banks in *Agathis australis* forest with occasional broadleaf and podocarp species. The type occurred with *Hymenophyllum armstrongii* and *Bazzania novae-zelandiae* at the base of a *Knightia excelsa* trunk at 245 m on Great Barrier Island.

Comments: A distinctive plant not to be confused with any of our other species. The plants are small, at most 770 μm wide and lack secondary pigments. No New Zealand *Acromastigum* has the combination of the reduced dorsal lobe, often being only a low, rounded or truncate projection (Fig. 89: 1), the exceedingly thick-walled cells that are larger in the median-basal sector of the leaf and form a subvitta of 2–3 rows (Fig. 89: 1) and the coarsely papillose surface present at least throughout the median and distal cells (Fig. 89: 4).

Acromastigum anisostomum (Lehm. & Lindenb.) A.Evans

[Plate 7D]

Jungermannia anisostoma Lehm. & Lindenb. *in* Lehm., Nov. Min. Cogn. Stirp. Pug. 6: 57. 1834. *Mastigobryum anisostomum* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, Syn. Hepat. 219. 1845. *Bazzania anisostoma* (Lehm. & Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 414. 1877. *Acromastigum anisostomum* (Lehm. & Lindenb.) A.Evans, Ann. Bryol. Suppl. 3: 48. 1934. Type: New Zealand, South Is., Dusky Bay, [*Menzies*], "Hb. Hooker" (STR!).

Jungermannia atro-virens Hook.f. & Taylor, London J. Bot. 3: 388. 1844. *Mastigobryum atro-virens* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 218. 1845. *Bazzania atro-virens* (Hook.f. & Taylor) Kuntze, Revis. Gen. Pl. 2: 832. 1891. Type: Auckland Is., ex herb. Jack (G!).

Acromastigum anisostomum var. *minutum* E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 71. 1965. Holotype: Stewart Is., near Cedric Creek, N. W. Arm, Paterson's Inlet, 29 Jan. 1949, *Martin* (herb. Hodgson no. 12151) (MPN!).

Plants stiff and wire-like, in pure colonies or mixed with other bryophytes, suberect to erect, yellowish to reddish brown (the stem often becoming deep red to blackish); plants when dry distinctly nitid and with leaves strongly ventrally deflexed; shoots small, to 0.8 mm wide. Branching pseudo-dichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf ± symmetric, ovate, undivided, vittate, tapering to a sharp apex; first branch underleaf 2–3-lobed, inserted on ventral-lateral side of juncture of main axis and branch. *Acromastigum*-type branches frequent, long and stoloniform. Ventral-intercalary branches lacking. Stem stiff and brittle, the cortical cells strongly differentiated, much larger than the medullary cells (ca. 2:1), in 7 rows, the radial walls thick-walled, the outer tangential walls also thickened, at times strongly so; medullary cells thinner-walled. Leaves rigid, imbricate, allowing little of stem exposed in dorsal aspect, spreading (ca. 60–80°), moderately convex, the apex moderately deflexed but the ventral lobes of opposing leaves not overlapping one another in ventral aspect; leaves vittate, 215–300 μm wide × 385–600 μm long, strongly incubous, asymmetrically ovate; apex unequally bilobed to ca. 0.2–0.35(0.45), the ventral lobe ca. 2× or less the dorsal in length, the lobes entire, terminating in a single cell or uniseriate row of 2 non-elongated cells; dorsal lobe acute, 5–7 cells wide at base; ventral lobe narrowly acute, 4–6 cells wide at the base and gradually tapering to the tip; dorsal margin ampliate, with a blunt tooth or rounded to subrectangular auricle at base, the basal sector often also with 1–2 slime papillae and a blunt tooth, the margin otherwise entire and extending to middle of stem or somewhat beyond; ventral margin nearly straight or somewhat incurved, sporadically subauriculate at base, entire. Cells of leaf distinctly thick-walled, those of ventral sector of leaf distinctly larger, forming a strong vitta running parallel to and 2–4 cells within the ventral margin; vitta 3–4 cells wide at base (or more in leaves with a ventral dilation), the cells with bulging to knot-like, often confluent trigones, 21–30 μm wide × 28–44 μm long; cells in dorsal sector of leaf much smaller, 12–18 μm wide × 15–21 μm long, uniformly thick-walled, without trigones; surface smooth. Oil-bodies (*fide* Schuster, 2000a, fig. 111) (2)4–8(16) per vitta cell, coarsely botryoidal, at times few segmented or homogeneous and smooth, 4–7 × 4–17 μm. Underleaves small and inconspicuous, distant, ± squarrose at base and becoming erect, convex, broadly elliptic to subrectangular, broader than long, deeply and ± equally 3-lobed to ca. 0.5; lobes 4–6 cells wide at base, the apex broadly rounded to retuse, entire, terminating in 2–4 laterally juxtaposed cells; disc margins somewhat ampliate, narrowing abruptly to the insertion, entire; cells of disc and lobes strongly thick-walled; surface smooth. Fungal partner absent.

Androecia and gynoecia not seen.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island (530 m), South Island (0–900 m), North Island (300–900 m); Australia: Tasmania, New South Wales. Known from Fiordland, Westland, Western Nelson, Southern North Island (Ruahine and Tararua ranges), Auckland (Coromandel, Little Barrier Island) and Northland (Waipoua) EPs.

This species, which at times may become locally abundant, often forms deep, pure, golden brown, intricately interwoven mats or mounds over peaty substrates, on decayed stumps and logs (particularly those that are bryophyte covered) and peaty ground in general, where not apt to be submerged. Regularly accompanying species in these habitats are *Adelanthus falcatus*, *Anastrophyllum schismoides*, *Bazzania nitida*, *Dicranoloma robustum*, *Hymenophyllum armstrongii*, *Kurzia hippuroides* and *Wijkia extenuata*.

Other species that are less often seen in association are *Acrobolbus lophocoleoides*, *Archeophylla schusteri*, *Chandonanthus squarrosus*, *Clandarium xiphophyllum*, *Ditrichum difficile*, *Heteroscyphus cymbaliferus*, *H. decipiens*, *Lepicolea attenuata*, *Lepidozia kirkii*, *L. setigera*, *Pulchrinodus inflatus*, *Radula scariosa* and *Schistochila ciliata*. Sometimes on tree bases mixed with *Acromastigum cavifolium*, *Herbertus oldfieldianus* and *Lepicolea*, and rarely epiphytic and with *Acrochila biserialis*, *Herbertus oldfieldianus* and *Hymenophyllum armstrongii*. It occasionally occurs in scattered to dense patches over bedrock (e.g., ca. 800–840 m in a protected valley below summit area of "Little Moehau," Coromandel Peninsula). On Stewart Island at 530 m in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs, and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus*. Accompanying species in semi-open habitats are *Anastrophyllum schismoides*, *Campylopus clavatus* and *Kurzia hippuroides*.

Comments: Despite the considerable variation in vigor and leaf form in *Acromastigum anisostomum*, this species is clearly separable from *A. mooreanum*, which has a much narrower, stiff, spur-like, lanceolate ventral leaf lobe vs. a shorter, more triangular ventral lobe in *A. anisostomum*. The leaves of the two species are otherwise very similar. In *A. anisostomum* the vitta is 2–3 cells wide and formed of cells that diminish in size from leaf base to apex. The cells are up to 35 × 50–65 μm basally, 28–32 × 45–55 μm subbasally and only 25–30 × 30–38 μm above and to either side. The cells along the ventral margin are smaller, but not nearly as small as in the anterior half of the lamina, where they become progressively smaller and average only 12–13 μm along the anterior leaf margin. The vitta cells have coarse trigones and thick longitudinal walls, but the transverse walls between successive cells are relatively thin. On either side of the vitta, the cells become more nearly equally thick-walled, with rounded rather than irregular and sinuous lumina.

Acromastigum mooreanum (Steph.) E.A.Hodgs.

[Fig. 90: 3, 4, oil-bodies, p. 410; Fig. 91]

Bazzania mooreana Steph., Hedwigia 33: 1. 1894. *Mastigobryum mooreanum* (Steph.) Steph., Sp. Hepat. 3: 539. 1909. *Acromastigum mooreanum* (Steph.) E.A.Hodgs., Trans. Roy. Soc. New Zealand 82: 19. 1954. Type: Tasmania, Jones Walk, Spreut (= Sprent) River, 600 ft., *Moore 65*, com. Ferd. v. Mueller (!).

Plants stiff and wire-like, suberect to erect, yellowish to reddish brown (the stem often becoming blackish); plants when dry distinctly nitid and with leaves strongly ventrally deflexed; shoots small, to 1.2 mm wide, subcircinate at the tip. Branching repeatedly pseudodichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf ± symmetric, ovate, undivided, nonvittate, tapering to a sharp apex; first branch underleaf 2–3-lobed, inserted on ventral-lateral side of branch at juncture of main axis and branch. *Acromastigum*-type branches common, stoloniform. Ventral-intercalary branches occasional, leafy. Stem stiff and brittle, the cortical cells strongly differentiated, much larger than the medullary cells (ca. 2.5:1), in 7 rows, the radial walls thick, the outer tangential walls strongly thickened; medullary cells thin-walled. Leaves stiff and brittle, imbricate, allowing little of stem exposed in dorsal aspect, widely spreading, strongly deflexed, the ventral lobes of opposing leaves often approximate in ventral aspect, the leaves moderately convex; leaves vittate, 260–305 μm wide × 600–720 μm long, strongly incubous, subfalcate, asymmetrically narrowly ovate; apex unequally bilobed to ca. 0.5, the ventral lobe 2–4× longer than the dorsal, the lobes

Fig. 90.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Acromastigum colensoanum* (Mitt.) A.Evans. Basal cell of leaf. 2. *Acromastigum colensoanum* (Mitt.) A. Evans. Vitta cell from midpoint of leaf. 3. *Acromastigum mooreanum* (Steph.) E.A.Hodgs. Cells of ventral lobe. 4. *Acromastigum mooreanum* (Steph.) E.A.Hodgs. Vitta cells. (Figs. 1, 2, from *Glenny 9174*, New Zealand, South Is., Westland EP, Mt. Te Kinga; 3, 4, from *Glenny 9605*, New Zealand, South Is., Western Nelson EP, Stockton Plateau.)

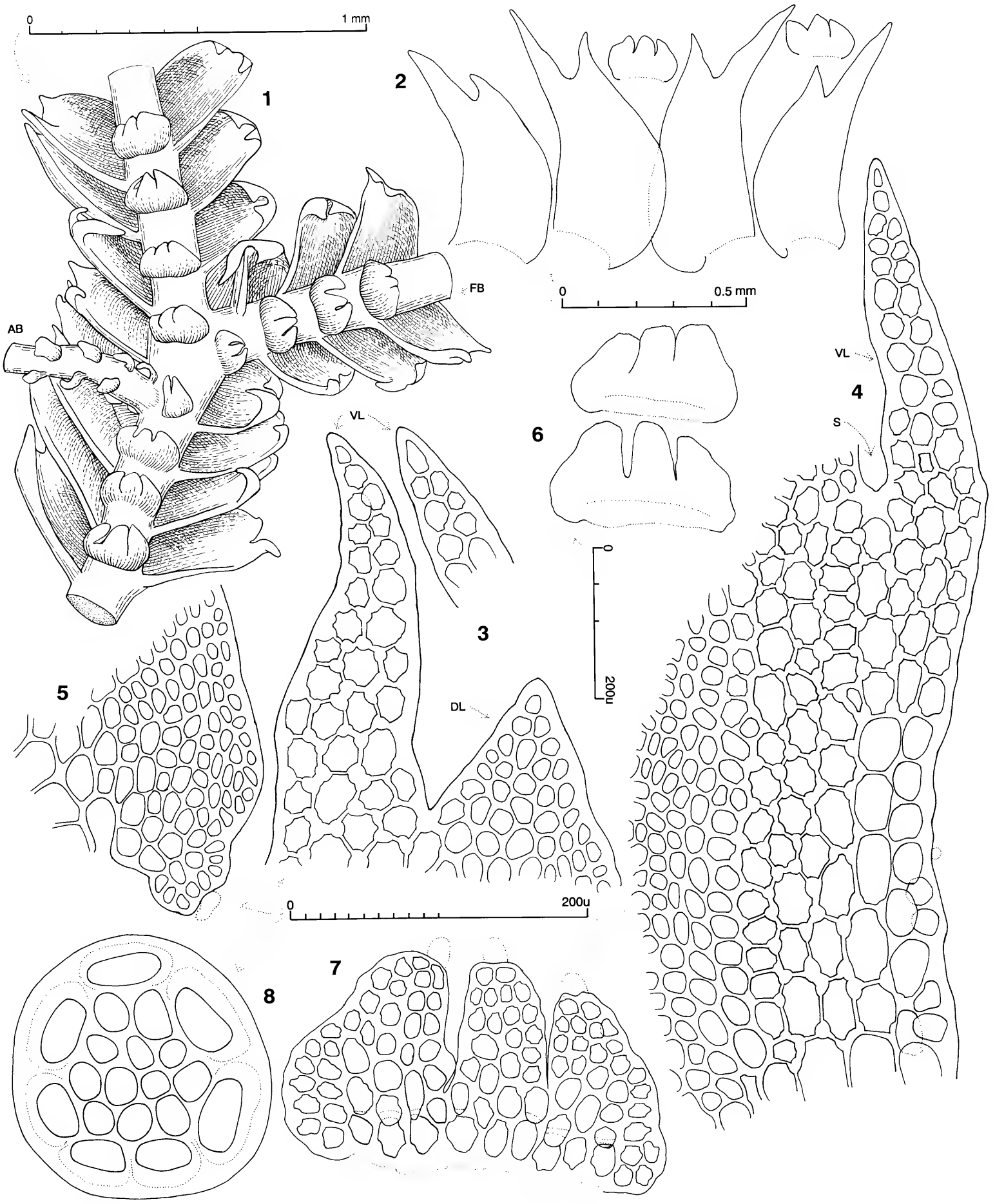

Fig. 91.
Acromastigum mooreanum (Steph.) E.A.Hodgs. 1. Portion of leading shoot with *Acromastigum*-type branch (= AB, note half-underleaf) and a *Frullania*-type branch (= FB), ventral view. 2. Leaves and above, underleaves at same scale. 3. Leaf apex (DL = dorsal lobe; VL = ventral lobe). 4. Ventral sector of leaf (VL = ventral lobe; S = sinus base); note well-defined vitta, and slime papilla (at arrow). 5. Portion of dorsal base of leaf showing auricle and slime papilla. 6. Underleaves, stipple above insertion indicates line formed by distal end walls of intermediate cells. 7. Underleaf, cellular detail. 8. Stem, cross section. (All from *Fife 6423*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., N flank of Mt. Euclid.)

entire; dorsal lobe acute, the cells often with trigones smaller than those of ventral lobe, the cells at times evenly thick-walled, the lobe 4–5 cells wide at base, terminating in a single cell or a uniseriate row of 2 cells; ventral lobe subulate, 3–4 cells wide at the base and biseriate for much of its length, terminating in a single cell or more commonly a uniseriate row of 2–3 cells, the terminal cell somewhat elongated, tapering to a point; dorsal margin somewhat ampliate, extending to middle of stem or somewhat beyond, cordate to auriculate, at times with a lobuliform auricle near insertion, the basal sector often also with 1–2 slime papillae, the margin entire or somewhat sinuate at the base; ventral margin nearly straight or somewhat incurved, with a slight basal dilation, entire. Cells of leaf with a strong vitta of distinctly larger, rectangular cells occupying the ventral half of leaf (and continuing into the ventral lobe) but without a distinct marginal row or rows of smaller, isodiametric cells, the vitta 4–5 cells wide in basal half of leaf; cells of vitta with knot-like trigones, 26–37 μm wide × 29–39(42) μm long; cells in dorsal sector of leaf becoming much smaller, isodiametric, 11–22 μm wide and long, uniformly thick-walled, without trigones; free walls of marginal cells of ventral lobe and ventral margin of disc strongly thickened; surface smooth. Oil-bodies pale smokey grey, 2–7(8) per vitta cell (6–12 per vitta cell *fide* Schuster, 2000a, fig. 111), 2–3 per non-vitta cell, broadly elliptic, coarsely and irregularly botryoidal, with age the spherules coalesce and the segments become fewer and the oil-body shape becomes subglobose. Underleaves rigid, small and inconspicuous, very firmly attached at a thick base, distant, ± squarrose at base and becoming erect, convex, broadly elliptic to subrectangular, much broader than long, deeply and ± equally 3-lobed to ca. 0.5; lobes 4–6 cells wide at base, the apex broadly rounded, entire, terminating in 2–4 laterally juxtaposed cells; disc margins cordate to subauriculate, narrowing abruptly to a narrow insertion; disc margins entire; cells of disc and lobes strongly thick-walled; surface smooth.

Androecia and gynoecia not seen.

Distribution and Ecology: New Zealand: Auckland Islands (15–55 m), Stewart Island (5–530 m), South Island (200–1050 m); Australia: Tasmania. In New Zealand known from Fiordland (Secretary Island) and North Westland (Paparoa Ra.) EPs.

In New Zealand known from several stations on Stewart Island and South Island. On Stewart Island it occurs in small bryophyte mounds deep in thickets within mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall; dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus* (Mt. Rocky summit area, 530 m). Also on ground under *Leptospermum* in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus* (Freshwater Landing, 5 m). Also on the sides of small cushions in open shrubland consisting of *Leptospermum scoparium*, *Olearia colensoi*, *Gahnia* and emergent *Podocarpus hallii* (Pryse Peak, 350–355 m). In the South Island occurring in Fiordland (Facile Harbor, *Allan* [MPN!] and Secretary Island) and in the Paparoa Mtns. (N flank of Mt. Euclid and ca. 0.5 km SE of Morgan Tarn, both at 1050 m) where it occurred with *Dicranoloma* on a granite ledge in a moist *Nothofagus menziesii – Dracophyllum traversii* forest. It is found with *Bazzania adnexa*, *B. involuta*, *Clandarium xiphophyllum*, *Heteroscyphus decipiens*, *Lepidozia ulothrix*, *Schistochila chlorophylla* and *Wijkia extenuata*.

Comments: *Acromastigum mooreanum* is apparently rather rare in New Zealand in comparison to the closely related *A. anisostomum*. The "crossed swords" formed by the greatly elongated, strongly ventrally deflexed and approximate ventral leaf lobes (seen in ventral aspect) will readily distinguish this species. A suite of features involving the vitta, the size and shape of the ventral lobe, and the leaf areolation also differentiate this species from *A. anisostomum*.

Acromastigum brachyphyllum A.Evans

[Fig. 85: 3; Fig. 92]

Acromastigum brachyphyllum A.Evans, Ann. Bryol. Suppl. 3: 60. *f. 12.* 1934. Holotype: New Zealand, South Is., Paparoa Ra., 3000 ft., *R. Helms* (Y!); isotype: (CHR 4948 ex herb. T. Kirk 251!).

Plants rigid and wire-like, in loose tufts or mats, the leaves yellowish to golden brown but often ± rust-colored basally, the stems reddish brown, the plants nitid when dry; shoots small, to 0.6 mm wide. Branching sparingly pseudo-dichotomously furcate or clearly lateral, of *Frullania* type, widely spreading; branch half-leaf ± symmetric, very wide ovate, undivided, tapering to a sharp apex (rarely bidentate), subauriculate at the base, with a median-basal field of larger cells; first branch underleaf 2-lobed, inserted on ventral-lateral side of juncture of main axis and branch. *Acromastigum*-type ventral branches occasional, stoloniform. Stem cortical cells in 7 rows, the radial and outer tangential walls very thick, the transverse walls thin, the cortical cells larger than medullary cells, in surface view the dorsal cortical cells large, sinuate-hexagonal, the ventral cortical cells smaller. Leaves small in proportion to stem, rigid, fragile, easily tearing, cochleariform, distant to contiguous, with much of stem exposed in dorsal aspect, obliquely spreading, when dry strongly ventrally deflexed and cupped, when moist moderately convex, the lobe tips deflexed and not visible in dorsal aspect, with scattered bistratose patches (at most in groups of 3–5 cells), frequently in the median dorsal sector, subvittate, 245–400 μm wide × 320–465 μm long, strongly incubous, asymmetrically orbicular-ovate; apex unequally bilobed to ca. 0.25, the ventral lobe longer and broader than the dorsal, the lobes acute to obtuse, terminating in a single cell or 2 superposed cells, entire; dorsal lobe 4–6 cells wide at base; ventral lobe 4–5 cells wide at the base, 2–4 cells long; dorsal margin strongly ampliate, cordate to ± auriculate at base, extending to middle of stem or somewhat beyond, entire or somewhat irregularly repand-denticulate at the base, sometimes with several large, spherical slime papillae; ventral margin nearly straight, entire, not decurrent. Underleaves small, about equal to the stem in width, distant, squarrose at base and becoming erect, slightly convex, broadly elliptic, ± equally 3-lobed to ca. 0.3–0.5, subequal or the median lobe smaller; lobes closely approximate, 4–7 cells wide at base, the apex rounded to truncate, entire, terminating in 2–4 laterally juxtaposed cells and ending in a spherical slime papilla; disc margins cordate to subauriculate, narrowing abruptly to the insertion; cells of disc and lobes strongly thick-walled; margins entire; surface smooth. Cells of leaf distinctly thick-walled, those of ventral sector of leaf larger, forming an indistinct vitta (subvitta) that is strongly ventrally displaced, the cells strongly thick-walled, with bulging, knot-like, often confluent trigones; cells of vitta 25–30 μm wide × 30–40 μm long; cells of the ampliate dorsal sector much smaller, ± evenly thick-walled, 7–13 μm wide × 12–14 μm long; surface smooth throughout. Oil-bodies in the vitta cells occupying a conspicuous portion of the cell lumen, pale smokey grey, 2–3(4) per cell, very coarsely botryoidal, the segments very thin and membranous, the segmentation irregular and uneven, with age the individual spherules considerably swollen and the oil-bodies becoming fewer segmented and ultimately smooth; nonvittate cells and distal cells of lobes with oil-droplets only.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (320–540 m). Known only from Westland (Omoeroa Saddle) and Western Nelson (Paparoa Ra. and Stockton Plateau) EPs.

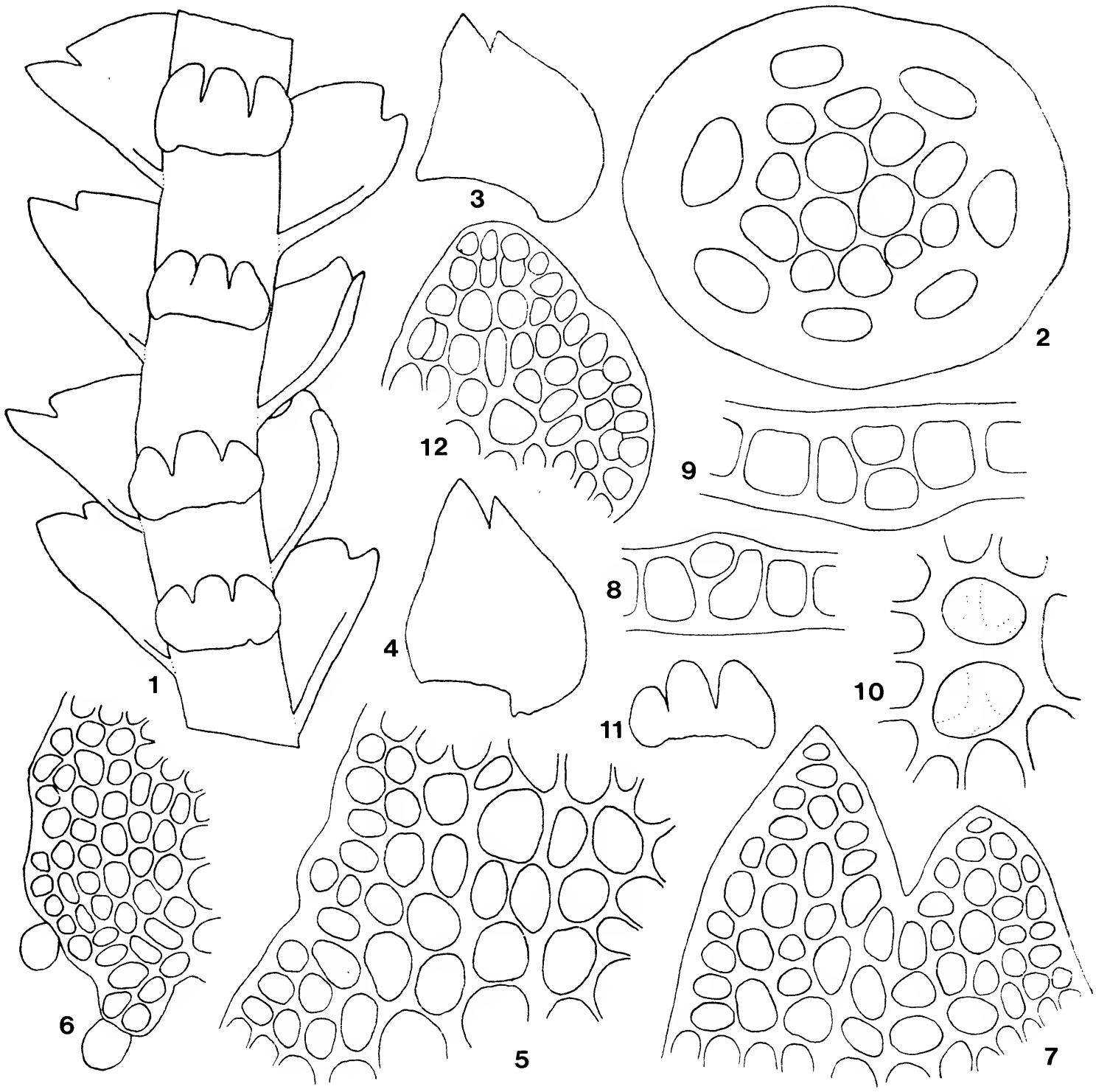

Fig. 92.
Acromastigum brachyphyllum A.Evans. 1. Part of plant, ventral view (× 62). 2. Cross section of branch (× 280). 3, 4. Leaves (× 62). 5. Cells from base of a third leaf, ventral side (× 280). 6. Dorsal base of a fourth leaf (× 280). 7. Apex of a fifth leaf (× 280). 8, 9. Leaf cells in cross section, showing bistratose condition (× 375). 10. Leaf cells in surface view, showing bistratose condition (× 375). 11. Underleaf (× 62). 12. Lateral lobe of a second underleaf (× 280). (All from type; after Evans, 1934.)

The Omoeroa Saddle collection is from peaty soil in *Lagarostrobos colensoi – Phyllocladus alpinus* shrubland with *Carpha alpina* and *Sphagnum cristatum* at 320 m. Accompanying species are *Adelanthus falcatus*, *Riccardia* and *Clasmatocolea*. The Stockton collection is from a wet overhanging bank under stunted *Nothofagus solandri* var. *cliffortioides – Phyllocladus alpinus* forest at 540 m, with *Acromastigum verticale*.

Comments: We know of no other *Acromastigum* with leaves at least locally bistratose (Fig. 92: 8–10). The presence of the bistratose condition in this species requires careful assessment, especially when compared to presence of that character in smaller phases of *A. anisostomum*. The species looks very similar to *A. anisostomum* in color and size of the plants, and further work needs to be done to establish its differentiation from that species.

Bazzania Gray

Bazzania Gray, Nat. Arr. Brit. Pl. 1: 704, 775. 1821, "*Bazzanius,*" *orth. cons.*

Plants strongly anisophyllous (except *Bazzania involuta*), typically firm, deep green to olive-green to yellow- or chestnut-brown, dull to highly nitid or (*B. tayloriana*) glaucous, milky and opaque, the shoots medium to robust in size, to 6 mm wide. Branching frequent, usually freely and repeatedly pseudo-dichotomous and never pinnate or (*B. involuta*) branching monopodial, the branches of *Frullania* type, normally originating from only one side of axis, subequal to main axis in vigor and with the main axis losing its dominance, branch half-leaf undivided, positioned in the fork of each "dichotomy"; first branch underleaf variable, asymmetrically or symmetrically 2–3(4)-lobed, rarely undivided, free or at times connate with a normal stem underleaf. Ventral branches all intercalary, occasional to frequent, often long and whip-like, stoloniform, geotropic, with scale-like leaves; ventral-intercalary leafy branches occasional to frequent. Stems rigid, with cortical cells often larger than the medullary, thick-walled, often ± evenly so. Rhizoids frequently at bases of reduced underleaves and leaves of geotropic stoloniform branches, less commonly from bases of underleaves on normal leafy shoots. Leaves alternate or subopposite (in ventral view), plane to moderately convex (the lobes often ± deflexed), widely spreading, the insertion distinctly incubous and extending to stem midline dorsally, the leaves typically ± asymmetrically ovate to falcate-rectangular, the dorsal margin commonly more arched and ampliate than the ventral; apex 2- or (in ours) 3-dentate (teeth sometimes obscure or almost lacking on weak shoots), at times with accessory teeth; dorsal margin (in ours) strongly arched, ampliate, at times cordate at base, entire or (rarely) denticulate; ventral margin typically ± straight or at times somewhat incurved, sometimes auriculate at base, entire or (rarely) denticulate (ciliate at the base in some extraterritorial species). Cells with walls slightly to distinctly thickened (especially in subapical sector of leaf), with trigones small to bulging and nodulose, the areolation ± uniform and without a vitta or the leaves subvittate (with a broad, indistinct band of enlarged cells in the median longitudinal portion of leaf), or the leaves distinctly vittate with several rows of sharply differentiated cells; surface smooth or papillose or (*B. tayloriana*) glaucous. Oil-bodies large for cell size, 2–6 per cell, homogeneous or at times few-segmented. Underleaves usually no more than 0.35–0.45× leaf area, or sometimes approaching the leaves in size in some species, free or connate with the leaves on one or both sides, variable, large and widely spreading to closely appressed to the stem and inconspicuous, ± quadrate to orbicular to transversely rectangular to reniform, the apex distinctly and regularly 4-lobed or truncate to rounded-truncate and variously lobulate, toothed or ragged, often with some or all of the cells decolorate and forming a hyaline distal sector, the base at times cordate. Asexual reproduction, when present, by caducous leaves and underleaves, also (*B. nova*) by regeneration from leaves.

Dioecious but often sterile, rarely with sporophytes. Androecia on short, ventral-intercalary branches from lower sectors of leading shoots and from both ventral and lateral sides of stoloniform branches, the androecia inconspicuous, tightly spicate; bracts concave to ventricose-cucullate to canaliculate, the apices truncate and entire to bidentate or bilobed; antheridia 1–2 per bract, the stalk biseriate; bracteoles smaller than bracts. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series largest, erect and closely ensheathing the perianth, the apices 2–4-lobed, the lamina margins usually variously crenate to dentate (in ours) or ciliate or laciniate-ciliate; bracteole similar in size and form. Perianth subfusiform, terete below, trigonous and plicate above, gradually narrowed toward

the usually contracted mouth; the mouth denticulate-dentate to subciliate; perianth usually multistratose below.

Seta usually with 10–16 outer cell rows and a central core of numerous, much smaller cells. Capsule ovoid to ovoid-oblong to long-ellipsoidal, the walls (3)4–6-stratose; outer layer of cells with two-phase development, the longitudinal walls with coarse, nodular thickenings that are sometimes confluent and then at least locally sheet-like alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls devoid of thickenings or sporadically have an isolated swelling; innermost layer of cells commonly with numerous semiannular bands.

Spores brown, with papillae and simple or furcate vermiculate markings, 1–1.25 to 2–3× the elater diam. Elaters rather rigid, nontortuous or at most feebly tortuous, long and slender, bispiral.

Type: *Bazzania trilobata* (L.) Gray (≡ *Jungermannia trilobata* L.)

A large genus of over 100 species worldwide, with particularly strong representation in tropical montane regions. For example, Fulford (1963b) records 54 species from Neotropical regions (all but *Bazzania skottsbergii* have stations in the tropics), but Gradstein et al. (2001) stated "probably no more than 40 species in tropical America." Grolle and Piippo (1984) record 53 species for New Guinea. Fulford (1946, 1959, 1963b) published useful revisions of the Neotropical and southern South American species. Two species occur in southern South America, *B. peruviana* (Nees) Trevis. and the pan-temperate *B. nitida* (F.Weber) Grolle (see Engel, 1978). *Bazzania chilensis* (Steph.) Fulford (see Fulford, 1963b, p. 125) is poorly known and needs further evaluation, and *B. skottsbergii* (Steph.) Fulford, while recognized by Fulford (1963b), is a synonym of *B. peruviana* (see Grolle, 1964a; Engel, 1978). Arnell (1963) included four species from South Africa, including *B. adnexa*, a species also present in our area. Nine species occur in New Zealand.

We do not recognize subgenera within the genus, and with regard to subgeneric categories, recognize only the section level, following arguments put forth by Schuster (1969c, 2000a).

References: Engel (2006b); Engel and Merrill (1994); Engel and Schuster (1988); Hodgson (1954; rev.); Schuster (2000a).

Key to Species

1a. Leaves clearly alternate, vittate, with a ± distinct strip of larger cells 3–4(6) cells wide running parallel to, and several cells within, the ventral margin of the leaf, the vitta cells with conspicuously bulging trigones; underleaves membranous, appressed to the stem, ± regularly (2)4-lobed or 4-dentate-lobulate (*B. monilinervis*) 2

2a. Plants glaucous, the leaves dull and opaque; leaf cell outlines obscured by a fine, granular coating. Underleaves 4-fid to 0.3, or ± bisbifid, the lobes bluntly rounded; plants fragile, easily broken when dry; branching often almost exclusively intercalary . . . . . *B. tayloriana* (p. 449)

2b. Plants green to olive-green (or brownish), the leaves ± translucent, not dull or opaque 3

3a. Underleaves connate on one side, about as wide as stem, divided into 4 distinct lobes (to ca. 0.5); leaf distinctly convex, the apex with teeth obscurely developed . . . . . *B. nitida* (p. 442)

3b. Underleaves free, to 2.5× stem width, wide elliptic to widely ovate or ± orbicular, very shallowly divided into small, irregular teeth or lobules; leaves plane to feebly convex, the apex with teeth well developed, distinct, spinulose, narrowly acuminate . . . . . *B. monilinervis* (p. 446)

1b. Leaves (in ventral aspect) opposite, not vittate as above, or at most subvittate (with a broad, indistinct band of enlarged cells in the median longitudinal portion of leaf, having more distinct trigones); underleaves conspicuous, with at least the basal half firm, ± spreading (often with apices and flanks at 90° to the stem, or more), the apex various but without discrete lobes (except *B. nova*) 4

4a. Plants subisophyllous (leaves and underleaves of about equal size); underleaves squarrose-reflexed, the margins broadly revolute, with much of the adaxial surface visible in ventral view. Plants erect, sparingly branched, the branching not pseudo-dichotomous . . . . . *B. involuta* (p. 418)

4b. Plants clearly anisophyllous; underleaves typically spreading to less than 90° (sometimes with only apices ± reflexed), with little if any of adaxial surface visible in ventral view 5

5a. Cells with trigones lacking or at most straight-sided and inconspicuous 6

6a. Terminal, *Frullania*-type branches exceedingly rare, a pseudo-dichotomous branch pattern thus lacking; leaves caducous; underleaves free on both sides, the apex shallowly 4–5-lobulate . . . . . *B. exempta* (p. 453)

6b. Terminal, *Frullania*-type branches frequent, freely and repeatedly pseudo-dichotomous; leaves persistent; underleaves connate on both sides, the apex entire or repand . . . . . *B. okaritana* (p. 434)

5b. Cells with trigones bulging to knot-like (at least in subvitta cells), or if small and concave-sided (some populations of *B. adnexa*), then with principal teeth at leaf apex typically with margins denticulate 7

7a. Underleaves ± regularly 4–6-lobed to ca. 0.3 (disc margins often with a prominent tooth in distal sector, the underleaf then appearing 6–8-lobed); underleaf lobes slenderly acuminate to spinulose; no hyaline cells present . . . . . *B. nova* (p. 439)

7b. Underleaves truncate to broadly rounded in outline, the apex ragged, sinuate-lobulate, or irregularly toothed (rarely subentire); hyaline, ± thin-walled cells often present (at least of underleaf apices) 8

8a. Underleaves longer than wide, subrectangular to lingulate, the apex truncate and irregularly crenate to subentire, the hyaline, thin-walled cells confined to a narrow border on both apex and lateral margins; leaf not subvittate, the areolation ± uniform throughout; leaf apex and margins of lamina quite entire, the principal teeth broadly triangular; plants robust (to 6 mm wide), the leaves 2.1–2.8 × 1–1.5 mm . . . . . *B. novae-zelandiae* (p. 436)

8b. Underleaves as wide as or wider than long, oblate to reniform (subquadrate in *B. hochstetteri*), the apex ragged, with irregular, crowded, sinuate teeth (rarely subentire), at least the distal sector of underleaf typically composed of hyaline, non-collenchymatous cells (sometimes occupying most of the underleaf); leaves subvittate, with a band of ± larger cells; plants medium to small (to 3.4 mm wide), the leaves 1–1.5 × 0.8–1 mm 9

9a. Leaves persistent, firmly attached, distinctly imbricate, the stem mostly hidden in dorsal aspect; leaf apex and distal margins of lamina serrulate (at least on some shoots); plants medium-sized, to 3.4 mm wide . . . . . *B. adnexa* (p. 423)

9b. Leaves often caducous, easily detached, loosely imbricate, with much of stem exposed in dorsal aspect; leaf apex and margins of lamina typically entire; plants small, to 1.8 mm wide . . . . . *B. hochstetteri* (p. 431)

Note: After the manuscript was prepared for publication Meagher (2003) reported *Bazzania accreta* (Lehm. & Lindenb.) Trevis. in New Zealand; the species was heretofore known only for Australia.

Sect. ***Protobazzania*** J.J.Engel

Bazzania sect. *Protobazzania* J.J.Engel, J. Hattori Bot. Lab. 99: 203. 2006. Type: *Bazzania involuta* (Mont.) Trevis. (≡ *Herpetium involutum* Mont.).

Bazzania involuta (Mont.) Trevis.

[Plate 8B; Fig. 93; Fig. 96: 1, 2, oil-bodies, p. 428]

Herpetium involutum Mont., Ann. Sci. Nat. II. 19: 253. 1843. *Jungermannia involuta* (Mont.) Hook.f. & Taylor *in* Hook.f., Bot. Antarc. Voy. 1: 159. 1845. *Mastigobryum involutum* (Mont.) Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 220. 1845. *Bazzania involuta* (Mont.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 414. 1877. Type: Auckland Is., *Hombron*.

Mastigobryum reflexistipulum Lindenb. & Gottsche, Sp. Hepat., fasc. 8–11: 102. 1851. *Bazzania reflexistipula* (Lindenb. & Gottsche) W.Martin & E.A.Hodgs. *in* W.Martin, Trans. Roy. Soc. New Zealand 78: 499. 1950. Type: Auckland Is., "(Hooker jun. in Hb. Gottsche)."

Mastigobryum elegans Colenso, Trans. & Proc. New Zealand Inst. 19: 288. 1887 (1886). *Bazzania involuta* fo. *elegans* (Colenso) Rodway, Tasman. Bryophy. 2: 74. 1916. *Bazzania elegans* (Colenso) W.Martin & E.A.Hodgs. *in* W.Martin, Trans. Roy. Soc. New Zealand 78: 499. 1950. Type: New Zealand, Waipawa Co., Mangatawhainui River, near Norsewood, 1881–86, *Colenso 1398* (G!).

Plants subisophyllous, large, ascending to stiffly erect in loose or rather dense cushions (anisophyllous, medium and prostrate to ascending in var. *submutica*), light green to pure and at times shiny green (especially in shade), becoming golden brown in sun; shoots to 3 mm wide, hooked at the tip. Branching infrequent, clearly lateral in position, smaller and much shorter than the main shoot, rarely pseudo-dichotomous, the branches of *Frullania* type; branch half-leaf ± symmetric, triangular-ovate, undivided and tapering to a sharp apex (occasionally shallowly bilobed), cordate to auriculate at base; first branch underleaf 2–3-lobulate, deeply concave-canaliculate and with broadly recurved-revolute margins, obliquely inserted on ventral or ventral-lateral side of main axis near base of branch, closely associated with but not connate with an underleaf of main axis, their adaxial surfaces approximate. Ventral-intercalary leafy branches sporadically present; stoloniform branches abundantly produced. Stems wiry, the cortical cells firm, with evenly thickened walls, small. Leaves rigid, opposite, strongly ven-

trally deflexed, distinctly imbricate, covering stem in dorsal aspect, widely spreading (ca. 90°), moderately convex; leaves subvittate, 1015–1230 μm wide × 1150–1420 μm long, distinctly incubous, broadly and asymmetrically ovate, occasionally broader than long, the apex transversely to obliquely truncate, distinctly narrow, only 0.25–0.4× the width of leaf at its widest point, coarsely and ± symmetrically 3-dentate, the principal teeth broadly acute to subacuminate, the middle tooth often largest (8–15 cells wide at base), the teeth terminating in a single cell or a uniseriate row of 2–3 cells, the terminal cell tapering to a sharp, thick-walled point, the apex otherwise sharply and irregularly denticulate (leaf apex shallowly tridentate and otherwise entire in var. *submutica*); dorsal margin strongly ampliate, distinctly arched, extending to middle of stem to slightly beyond, cordate to auriculate at base, not decurrent, the margin entire or denticulate in distal half; ventral margin moderately curved, somewhat dilated to auriculate at base, entire or denticulate. Cells of leaf differentiated into a broad, diffuse band of enlarged rectangular cells in the median longitudinal portion of the leaf (subvittate), the cells much smaller near the margins, particularly the dorsal; median cells 20–29 μm wide × 30–41 μm long, moderately thin-walled, with straight-sided to bulging to knot-like trigones, intermediate thickenings often present; surface papillose in the distal half of leaf. Oil-bodies in the subvitta cells occupying a conspicuous portion of the cell lumen, pale smokey grey, 2–3(4) per cell, homogeneous, with various indentations, furrows and a few weak, thin, membranous segments, the segmentation irregular and uneven, with age the individual spheres swell considerably and the oil-bodies then become fewer-segmented and ultimately smooth; nonvittate cells and distal cells of lobes with oil-droplets only. Underleaves conspicuous, 3.6–4× stem width (when flattened), firm, squarrose-reflexed, deeply concave-canaliculate, resembling a scallop shell, the margins broadly recurved, the adaxial surface broadly exposed, often conspicuously connate with the leaves on both sides, ± reniform, wider than long, sometimes with a median sulcus, particularly when proximal to a branch (underleaves small, moderately spreading, hemispherical and narrowly revolute in var. *submutica*); apex and margins irregularly lobulate and sharply toothed like the margins of the leaves (occasionally edentate, particularly in var. *submutica*), without a distinct border of thin-walled, hyaline cells (or merely the teeth hyaline, or at most with an intermittent strip of hyaline cells 1(2) cells wide; median cells ± elongate-rectangular (ca. 18 μm wide and thus narrower than those of the leaves); surface papillose.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Campbell Island, Auckland Islands, Stewart Island (5–640 m), South Island (60–1340 m), North Island (670–1310 m). Known from Rakiura (Stewart Island, Muttonbird Islands), Fiordland, Southland, Westland, Canterbury (upper Wilberforce River), Otago (Mt. Cargill, Ajax Swamp, Lakes ER), Western Nelson (Arthur Ra., Marino Mtns., Paparoa Ra.), Sounds–Nelson (Richmond Ra., Mt. Stokes), Southern North Island (Ruahine and Tararua ranges), Volcanic Plateau (Tongariro Natl. Park), Taranaki (Mt. Taranaki), Gisborne (Urewera) and Auckland (Little Barrier Island, Coromandel Peninsula) EPs. Uncommon in the North Island, but widespread in the wetter parts of the South Island.

A species with a broad altitudinal range. It occurs in wet, rich forests, especially those with *Nothofagus* species present, from near sea level to treeline. The species occurs on bryophyte-covered old logs and rather commonly on tree bases, where it may form large masses. In particularly humid forests it forms masses on bryophyte-covered tree trunks, such as the rich, lowland forests of the Jackson River area (South Westland). The species is also terricolous, particularly where the forest floor is densely covered with bryophytes, and in such sites may

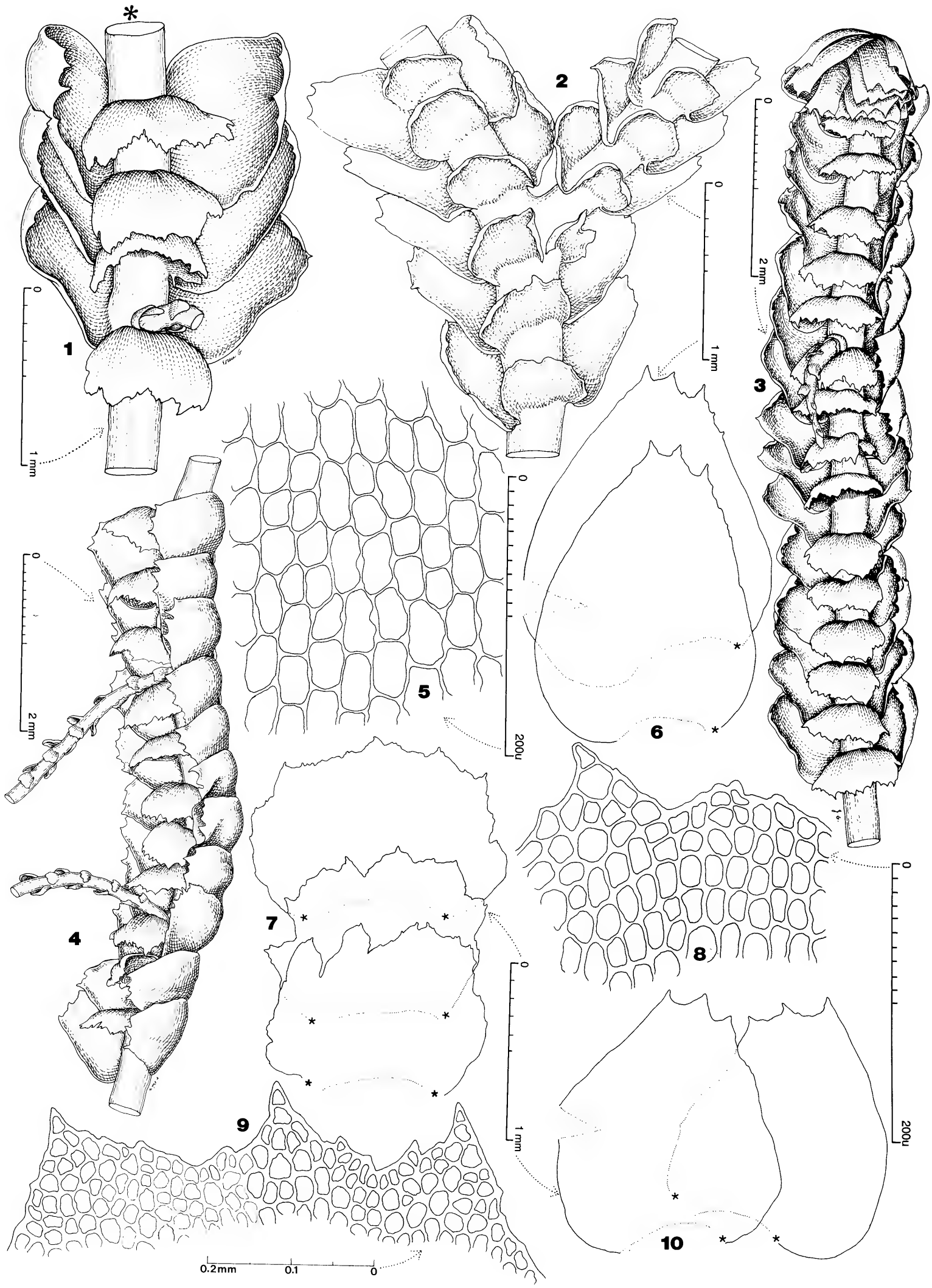

Fig. 93.
Bazzania involuta (Mont.) Trevis. (figs. 1, 3–10, var. *involuta*; 2, var. *submutica*). 1. Portion of main shoot with ventral-intercalary branch. 2. Junction of branch and main shoot, ventral view; note first branch underleaf and main shoot underleaf are free from one another. 3. Portion of main shoot, ventral view. 4. Portion of main shoot, ventral-lateral view. 5. Median leaf cells. 6, 10.

form extensive patches (at times of ca. 1 m^2). Also on banks covered with bryophytes or bryophytes and hymenophylls. Also present in the penalpine zone, typically over damp leaf litter under *Chionochloa* tussocks.

Comments: Well-developed plants of this species are the easiest of the opposite-leaved New Zealand species of *Bazzania* to recognize because of the large, petaliform, squarrose-reflexed underleaves, the subisophyllous condition and the erect habit of growth. The underleaf margins are not ragged, but rather very coarsely serrulate (studded with spinose teeth). In addition, the branches are obviously lateral in position (rather than pseudo-dichotomous) and are typically smaller and much shorter than the main shoot. The first branch underleaf is transversely inserted and laterally aligned with an underleaf of the main axis; the margins of both are strongly reflexed, so that their adaxial surfaces are closely approximate ("back-to-back"), but not connate. Although long associated with *B. adnexa* (cf. Lindenberg & Gottsche, 1851, *sub Mastigobryum novae-hollandiae*), the expression known as var. *submutica* is better understood as a variety of *B. involuta*, as suggested by Hodgson (1954). While it is always possible to identify this species, in particular to separate it from *B. adnexa*, it is more difficult to assign specimens that come from forested habitats to one or other variety. Variety *submutica* may be differentiated from the typical variety as follows:

Key to Varieties

1a. Plants robust, stiffly erect, subisophyllous; underleaves squarrose-reflexed, large and petaliform, the apex and margins broadly recurved, ± lobulate and often sharply toothed; leaf apex coarsely tridentate, the principal teeth and sinuses typically with accessory teeth . . . . . var. *involuta* (p. 421)

1b. Plants medium, prostrate to ascending, clearly anisophyllous; underleaves moderately spreading, small and hemispherical, the apex and margins narrowly revolute, subentire; leaf apex shallowly tridentate, otherwise entire . . . . . var. *submutica* (p. 422)

Bazzania involuta (Mont.) Trevis. var. ***involuta***

[Fig. 93: 1, 3–10; Fig. 96: 1, 2, oil-bodies, p. 428]

Plants robust, shoots 1.3–2.1 mm wide, ascending to stiffly erect, isophyllous; first branch underleaf free, transversely inserted; leaves strongly imbricate, usually strongly deflexed; leaf apex coarsely tridentate, typically with accessory armature, the leaf margins often denticulate; underleaves squarrose-reflexed, large and petaliform, the margins broadly recurved, ± lobulate and often sharply toothed.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island (5 m), South Island (sea level–1310 m), North Island (720–1230 m), Chatham Islands; Australia: Tasmania.

Ecology: On wet grass litter in *Chionochloa antarctica*, *C. pallens*, *C. rubra*, *Schoenus pauciflorus* tussocklands and in mosaics of scrub and tussockland, often in wet depressions

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Leaves (flattened). 7. Underleaves (flattened). 8. Portion of underleaf apex. 9. Leaf apex. (Figs. 1, 3–10, from *Child 2586*, New Zealand, South Is., Westland EP, Key Summit [F]; 2, from *Hodgson s.n.* as *B. elegans*, New Zealand, North Is., Gisborne EP, Lake Waikareiti [F].)

and on tarn margins. Also on humus and under scrub (penalpine in North and South islands, but extending to sea level in the subantarctic islands) of *Halocarpus biformis*, *Dracophyllum longifolium*, *D. scoparium*, *Leptospermum scoparium*, *Myrsine divaricata*, *Olearia colensoi*, *O. lyallii* and *Podocarpus nivalis*. Sometimes in upper montane *Nothofagus solandri* var. *cliffortioides* forest. On Stewart Island (Freshwater Landing, track to Mason Bay, 5 m), in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. Associated species are *Acrobolbus lophocoleoides*, *Adelanthus occlusus*, *Blepharidophyllum vertebrale*, *Clandarium xiphophyllum*, *Cuspidatula monodon*, *Dicranoloma robustum*, *Gackstroemia alpina*, *Herbertus oldfieldianus*, *Kurzia hippuroides*, *Lepidozia obtusiloba*, *Riccardia perspicua* and *Trichotemnoma corrugatum*.

Bazzania involuta var. ***submutica*** (Lindenb. & Gottsche) J.J.Engel & Merrill

[Fig. 93: 2]

Mastigobryum novae-hollandiae f. τ 3 *submuticum* Lindenb. & Gottsche, Sp. Hepat. fasc. 8–11: 33, 46. 1851 ("*submutica*"). *Bazzania involuta* fo. *submutica* (Lindenb. & Gottsche) E.A.Hodgs. *ex* Hamlin, Rec. Domin. Mus. 7: 251. 1972. *Bazzania involuta* var. *submutica* (Lindenb. & Gottsche) J.J.Engel & Merrill, Bryologist 97: 314. 1994. Type: New Zealand, South Is., Dusky Bay, "in hb. n. 15" (S!).

Plants medium, prostrate to ascending, shoots 1–2.4 mm wide, compact, clearly anisophyllous; first branch underleaf often free, obliquely inserted; leaf apex shallowly tridentate, otherwise entire, the leaf margins entire; underleaves moderately spreading, small and hemispherical, the margins narrowly revolute, subentire. Oil-bodies at midleaf 2–3 per cell, homogeneous, smooth surfaced, colorless, spherical and 4–7 μm in diam. to ellipsoidal and 4–8 × 5.5–12 μm; oil-bodies at base of leaf 2–6 per cell, homogeneous but surface like a potato when large, ellipsoidal and 5–8 × 11–14.5 μm or spherical and 5–7 μm in diam.

Distribution and Ecology: Endemic to New Zealand: South Island (sea level–890 m), North Island (945–1100 m). Known from Otago (Mt. Cargill), Westland (Haast, Paringa River, Nelson Lakes Natl. Park), Southern North Island (Eastbourne, Rimutaka Ra., Tararua Ra., Ruahine Ra.), Gisborne (Urewera Natl. Park), Auckland (Coromandel Peninsula, Little Barrier Island) and Northland (Waipoua Forest) EPs.

On humus, tree stumps, rotten logs and tree bases under forest, mainly in pure *Nothofagus solandri* var. *cliffortioides* forest, but also *N. solandri* var. *cliffortioides* forest mixed with *N. menziesii*, *N. fusca* and *Metrosideros umbellata*. Associated species are *Bazzania adnexa*, *Chandonanthus squarrosus*, *Clandarium xiphophyllum*, *Dicranoloma menziesii*, *D. robustum*, *Distichophyllum pulchellum*, *Heteroscyphus cuneistipulus*, *Hymenophyllum bivalve*, *Hypnum cupressiforme*, *Leifidium tenerum*, *Lepicolea attenuata*, *L. scolopendra*, *Leucobryum candidum*, *Plagiochila circinalis*, *P. deltoidea*, *P. fasciculata*, *Pyrrhobryum mnioides*, *Trichocolea mollissima*, *Weymouthia cochlearifolia* and *Wijkia extenuata*. The var. *submutica* only sporadically occurs in the penalpine zone, whereas var. *involuta* often is found above treeline under penalpine scrub and tussockland.

Comments: This is a relatively common plant, which differs from typical *Bazzania involuta* in having narrower shoots and much smaller underleaves, which are only moderately spread-

ing, narrowly revolute and subentire. The plants have a distinctive "channeled" appearance in ventral aspect, with crowded, densely imbricate leaves and a yellow-green color (in the dried condition) that resembles that of typical *B. involuta*. When fresh, the plants are yellow-green, the same color as often seen in *B. adnexa*, whereas typical *B. involuta* is usually straw-yellow when fresh.

The var. *submutica* can be confused with poorly developed expressions of *Bazzania adnexa*, but the absence of pseudo-dichotomous branching, the form of the first branch underleaf, and the underleaf and its areolation are helpful in distinguishing the variety. Plants of *B. adnexa* typically have underleaves with ragged, broadly hyaline margins (Fig. 94: 6, 7, 10) and "butterfly type" first branch underleaves that are marginally connate with an underleaf of the main shoot (Fig. 95: 1). The leaves of var. *submutica* are convex from the dorsal view, while those of *B. adnexa* are more plane.

Sect. ***Connatae*** (Steph.) Fulford

Mastigobryum sect. *Connatae* Steph., Hedwigia 25: 245. 1886.
Bazzania sect. *Connatae* (Steph.) Fulford, Ann. Cryptog. Phytopathol. 3: 103. 1946.

Bazzania adnexa (Lehm. & Lindenb.) Trevis.

[Figs. 94, 95]

Jungermannia adnexa Lehm. & Lindenb. *in* Lehm., Nov. Min. Cogn. Stirp. Pug. 4: 58. 1832. *Mastigobryum adnexum* (Lehm. & Lindenb.) Mont., Voy. Pôle Sud. Bot. 1: 243. 1845. *Bazzania adnexa* (Lehm. & Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 414. 1877. Type: Australia.

Jungermannia novae-hollandiae Nees *in* Hook.f., Bot. Antarc. Voy. 1: 159. 1845. *Mastigobryum novae-hollandiae* (Nees) Nees *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 221. 1845. *Bazzania novae-hollandiae* (Nees) Carrington & Pearson, Pap. & Proc. Roy. Soc. Tasmania 1887: 50. 1888. Type: Auckland Is.

Mastigobryum semicordatum Lindenb. & Gottsche *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 720. 1847. *Bazzania semicordata* (Lindenb. & Gottsche) Kuntze, Revis. Gen. Pl. 2: 832. 1891. Type: Auckland Is. and Campbell Is., *Hooker*.

Mastigobryum macro-amphigastrum Colenso, Trans. & Proc. New Zealand Inst. 19: 289. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso*.

Mastigobryum olivaceum Colenso, Trans. & Proc. New Zealand Inst. 19: 290. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso*.

Mastigobryum polyodon Colenso, Trans. & Proc. New Zealand Inst. 19: 291. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso*.

Mastigobryum compactum Colenso, Trans. & Proc. New Zealand Inst. 19: 291. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso a. 1406* (BM!, WELT!).

Mastigobryum macrodontum Colenso, Trans. & Proc. New Zealand Inst. 19: 292. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso*.

Mastigobryum nitens Colenso, Trans. & Proc. New Zealand Inst. 19: 293. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso a. 1409* (WELT!).

Mastigobryum parasiticum Colenso, Trans. & Proc. New Zealand Inst. 19: 293. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso*.

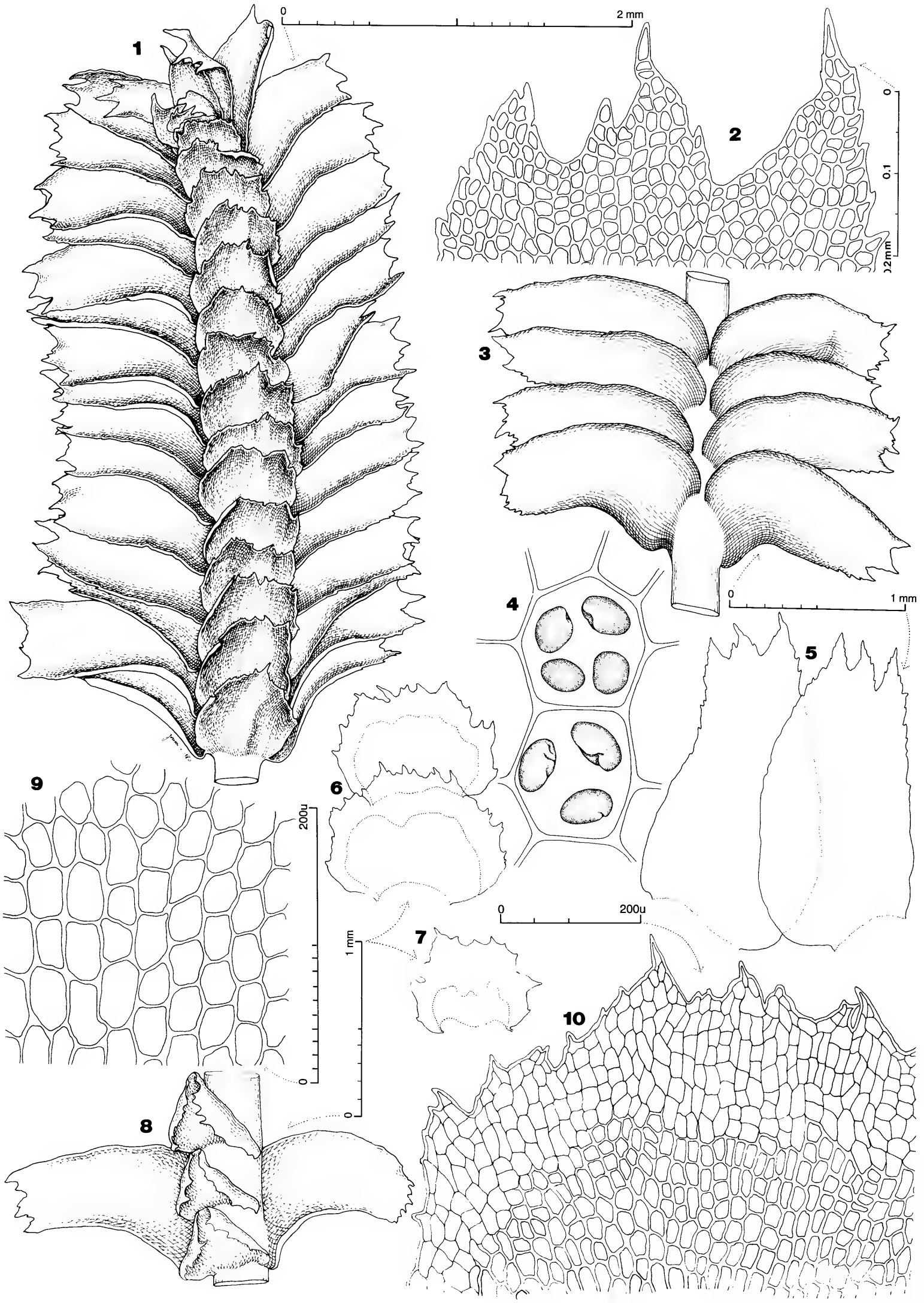

Fig. 94.
Bazzania adnexa (Lehm. & Lindenb.) Trevis. (figs. 1–6, 9, 10, var. *adnexa*; 7, 8, var. *aucklandica*). 1. Portion of main shoot, ventral view. 2. Distal sector of leaf. 3. Portion of main shoot, dorsal view. 4. Oil-bodies of median leaf cell (× 665). 5. Leaves. 6, 7. Underleaves; stipple indicates region of

Mastigobryum heterodontum Colenso, Trans. & Proc. New Zealand Inst. 21: 66. 1889 (1888). Type: New Zealand, Wairoa Co., woods near Lake Waikare, 1888, *Hill*.

Mastigobryum vulcanicum Colenso, Trans. & Proc. New Zealand Inst. 21: 67. 1889 (1888). Type: New Zealand, East Taupo Co., Mt. Tongariro, 1887, *Hill*.

Bazzania lacerata Steph., Hedwigia 32: 209. 1893. *Mastigobryum laceratum* (Steph.) Steph., Sp. Hepat. 3: 478. 1908. Type: New Zealand, Great Barrier Is., *Kirk 214* (G!).

Mastigobryum kirkianum Steph., Sp. Hepat. 3: 455. 1908, *syn. nov*. Type: New Zealand, Great Barrier Is., *Kirk 152*, *153* (G!).

Mastigobryum adnexum fo. *exarmatum* Steph., Sp. Hepat. 3: 479. 1908 ("*exarmata*"). Type: "Australia, Tasmania valde communis; New Zealand haud rara; Africa, Table Mountain prope Capetown bene quadrat."

Plants strongly anisophyllous, sprawling to suberect in loose cushions or mats, yellow-green to deep green to brownish green; shoots medium-sized, to 3.4 mm wide. Branching repeatedly pseudo-dichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf ± symmetric, narrowly ovate or ovate-lanceolate, undivided, tapering to a sharp or bidentate, serrulate apex; first branch underleaf 2–3-lobulate, subtransversely inserted on ventral side of main axis somewhat below base of branch, usually marginally connate at base to an underleaf of main axis or less commonly free, but with bases ± juxtaposed. Ventral-intercalary leafy branches sporadically produced, at times mimicking the terminal branches; stoloniform branches abundantly produced. Stems stiff, the cortical cells small, firm, with evenly thickened walls or the longitudinal walls very thick and the transverse walls thin. Leaves opposite, horizontal to ventrally deflexed, distinctly imbricate, with little or none of stem exposed in dorsal aspect, widely spreading (ca. 90°); leaves not vittate, 910–1120 μm wide × 1470–1890 μm long, distinctly incubous, asymmetrically ovate-ligulate, falcate, the apex rather broadly truncate, the truncation square to oblique, the apex often somewhat plicate, coarsely and ± symmetrically 3-dentate, the principal teeth broadly acute to apiculate to subacuminate, 2–7 cells wide at base, the teeth terminating in a single cell or a uniseriate row of 2–3 cells, the terminal cell tapering to a sharp, thick-walled point, the tooth margins and intervening sinus bases sharply and irregularly denticulate (occasionally edentate); dorsal margin strongly ampliate, distinctly arched and defining a broad crescentic line, extending to middle of stem or slightly beyond, cordate at base, the margin entire or denticulate in distal half; ventral margin straight to curved gently inward, somewhat dilated and subcordate at base, entire or denticulate. Cells of leaf differentiated into a broad, diffuse band of enlarged rectangular cells in the median longitudinal portion of the leaf (subvittate), the cells much smaller near the margins, particularly the dorsal; median cells 23–33 μm wide × 35–44 μm long, thin-walled, trigones variable: small and concave-sided to knot-like, intermediate thickenings sporadic; surface smooth or the teeth often finely papillose. Oil-bodies occupying a conspic-

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hyaline border of thin-walled cells; note 2 underleaves (above) are connate on both sides, the underleaf below (var. *aucklandica*) is narrowly connate at right base and free and subauriculate at left. 8. Portion of main shoot, ventral view. 9. Median leaf cells. 10. Distal sector of underleaf; note basal thick-walled cells and distal border of thin-walled, hyaline cells; note also the thickened exposed wall of underleaf apex and margin. (Figs. 1–3, 5, 9, from *Engel 12795*, Tasmania, Myrtle Forest, SW of Collinsvale; 4, from *Engel 20203*, same loc.; 6, 10, from *Engel 19266*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., Tiropahi R.; 7, from *Child H1017*, New Zealand, South Is., Otago EP, Mt. Cargill; 8, from *Hatcher 152*, New Zealand, North Is., Auckland EP, Waitakere Hills.)

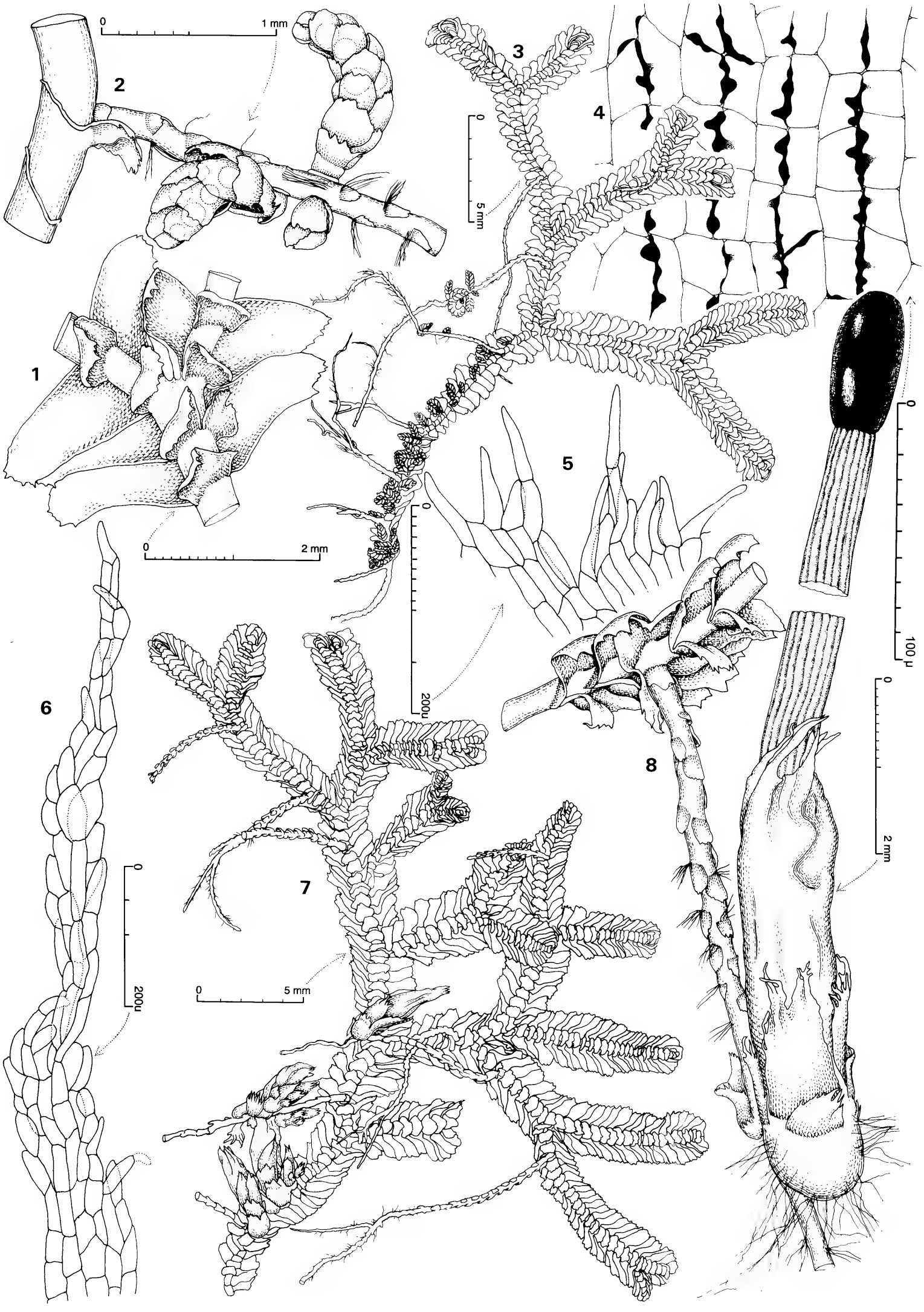

Fig. 95.
Bazzania adnexa (Lehm. & Lindenb.) Trevis. 1. Junction of branch and main shoot, note position of first branch underleaf and its juxtaposition with main shoot underleaf (second from shoot base). 2. Two mature androecia originating from a stoloniferous branch. 3. Plant showing position of an-

uous portion of cell lumen, dull opaque, with a cloud-like appearance, 2–3(4) to (2)3–5 per median leaf cell, 3–5 per in subvitta cells, 6–8(11) per basal cell, potato-shaped, ovoid to broadly elliptic, often irregularly so, to at times sausage-shaped, homogeneous, but the oil-body contents often not consistent throughout and appearing to possess folds, indentations or auriculations, the oil-bodies 7.2–8.5 × 9.1–11.7 μm, a few 7.8 × 12.4–13 μm. Underleaves conspicuous, erect to spreading, connate with the leaves on both sides (feebly connate or free at least on one side in var. *aucklandica*), subquadrate to oblate to reniform (or in var. *aucklandica*, triangular and tapering to a sharply channeled apex, the lateral margins sharply reflexed), broader than long, the apex distinctly ragged and hyaline (decolorate), with irregular, sharp, often crowded, sinuate teeth (rarely subentire), the hyaline distal sector variable in width, often occupying as much as half of underleaf or (var. *aucklandica*) very broad and with the green, thick-walled cells few and restricted to the median basal area, the hyaline sector composed of thin-walled, sinuate-rhomboidal cells; base straight or (var. *aucklandica*) cordate to subauriculate and with a narrow hyaline margin extending to the insertion; median non-hyaline cells quadrate to ± elongate; surface of hyaline cells very delicately papillose. Fungal partner absent.

Androecia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from leading shoots and both ventral and lateral sides of stoloniform branches; bracts ventricose-cucullate, the apex retuse to 2(3)-dentate; dorsal margin of disc slightly dilated, crenate-sporadically denticulate, the teeth unicellular, the margin sporadically smooth and merely with a few slime papillae; antheridia 1–2 per bract, the stalk biseriate; bracteolar antheridia present or absent. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem, the gynoecium base swollen and rhizoidous; bracts of innermost series much larger than leaves, erect and closely ensheathing the perianth, the bracts concave, ovate to subrectangular; apices with 4 main long lobes, each lobe either simple or in turn subdivided into 2 prominent lobules, the lobes or lobules markedly leptodermous, each subcaudate and with the distal sector consisting of a rather long biseriate region with the cell tips often variously projecting, the lobe-lobule biseriate to the tip or the tip composed of a uniseriate row of at most 3 cells, the lobe-lobule margins sparingly dentate-ciliate below the biseriate area; lamina composed of ± regularly short- to long-rectangular, leptodermous cells, the margin bordered by cells of variable shape, some only slightly longer than wide, others long and narrow, the apical or free end of marginal cells often divergent and forming a short projection or a tooth, the margin irregularly and rather copiously crenate-dentate, but often with a few short to long cilia; bracteole similar in size and form. Perianth prominent, straight to curved, fusiform, terete below, the distal half pluriplicate and gradually narrowing to the contracted mouth, the mouth irregularly dentate-subciliate, the processes composed of 1 or 2 superposed cells that are thin-walled, elongate and often completely laterally free; perianth ca. 9–10 stratose in basal sector.

Seta with 15 rows of outer cells, the interior cells not seen. Capsule rather long-ellipsoidal, the wall 70–74 μm thick, of 5–6 layers that are subequally thick or the outer layer feebly thicker; outer layer of cells very small, 16–19 μm wide × 28–36 μm long, with two-phase

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droecia and pattern of vegetative branching. 4. Capsule wall, outer layer. 5. Portion of perianth mouth. 6. ♀ Bract lobe. 7. Plant showing position of gynoecia and pattern of vegetative branching. 8. Gynoecium and mature sporophyte. (Fig. 1, from *Engel 19266*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., Tiropahi R.; 2–8, from *Engel 18741*, New Zealand, South Is., Fiordland EP, above South Branch of Borland Burn.)

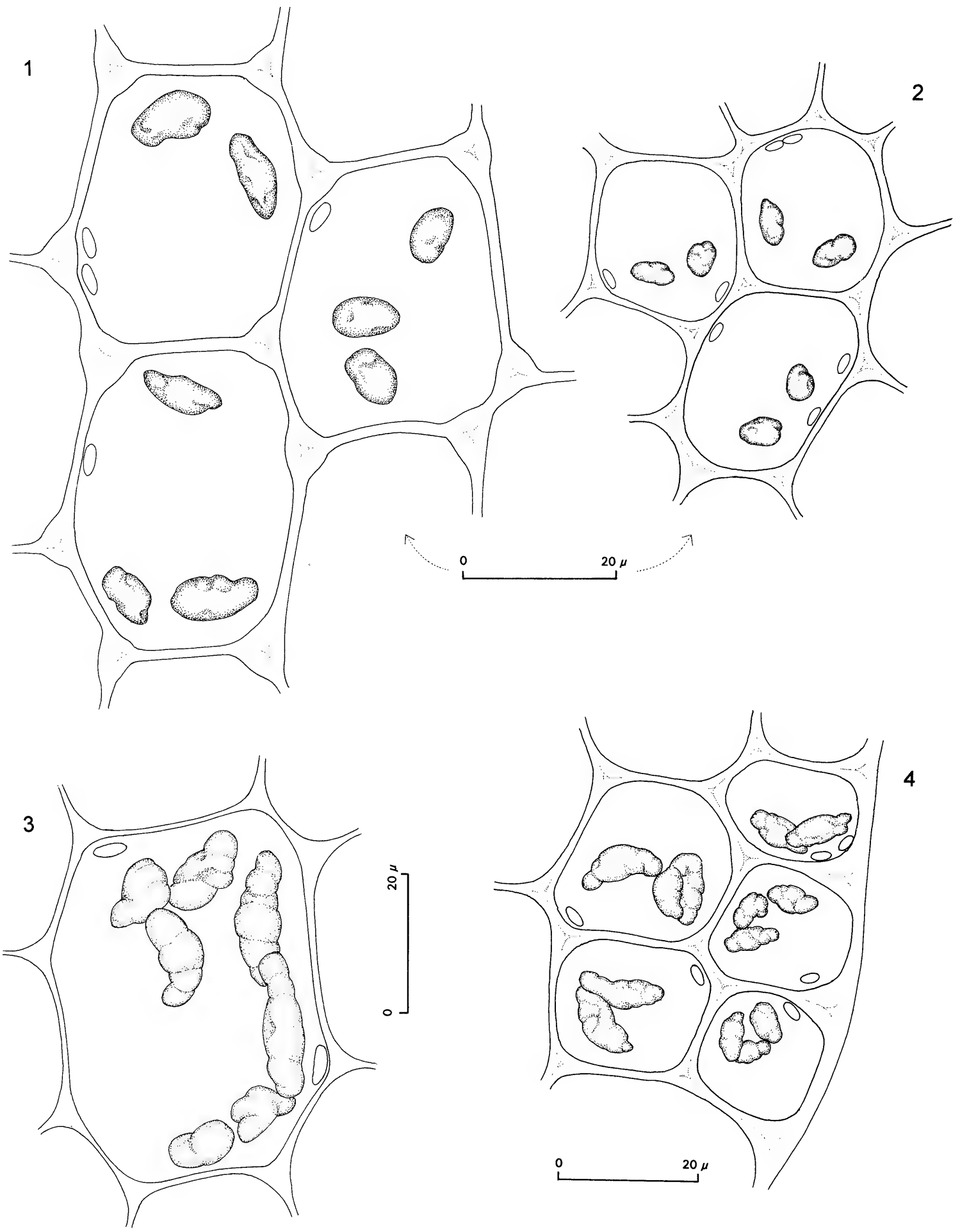

Fig. 96.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Bazzania involuta* (Mont.) Trevis. Subvitta cells in median sector of leaf. 2. *Bazzania involuta* (Mont.) Trevis. Inframarginal cells of dorsal, dilated portion of leaf. 3. *Bazzania okaritana* Meagher & Glenny. Cells of median sector of leaf. 4. *Bazzania okaritana* Meagher & Glenny. Marginal and submarginal cells (dorsal-median sector). (Figs. 1, 2, from *Glenny 9199b*, New Zealand, South Is., Westland EP, Upper Otira Valley; 3, 4, from *Glenny 9191*, type.)

development, the longitudinal walls with very thin, feebly developed, sheet-like thickenings and a few large nodule-like to spine-like thickenings alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls devoid of thickenings or sporadically have an isolated nodule; innermost layer of cells with ± tiered, irregularly narrowly to broadly rectangular cells, with semiannular bands common, rather wide, close, usually complete, rather frequently forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 16.8–19.7 μm in diam., brown, with dense, sharply defined papillae and abundant simple or furcate vermiculate markings. Elaters rigid, nontortuous, 9.1–11.5 μm wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.8–4.8 μm wide.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island (0–500 m), South Island (0–1070 m), North Island (180–915 m), Chatham Islands; Australia: Tasmania, Victoria, New South Wales, Queensland. In the South Island found at over 1000 m in Nelson and Marlborough, but in Fiordland only reaching ca. 600 m. Very widespread and common and recorded from all provinces, but it is known from a single Marlborough record (Mt. Robertson), a single Canterbury record (Wilberforce River) and records from Otago are from only the Otago Coast and Lakes ERs.

All records are from either forest or scrub with a closed canopy. Forest types include *Agathis australis* forest, tall podocarp forest, sometimes mixed with *Nothofagus* and *Weinmannia*, all types and mixtures of *Nothofagus* forest, *Knightia excelsa – Beilschmiedia tawa* forest and *Weinmannia racemosa – Metrosideros umbellata* forest. Not recorded from scrub, shrub-tussockland, or tussockland above the treeline.

Found on stumps, rotten logs, humus, tree bases and on trunks of tree ferns (*Dicksonia* and *Cyathea*), particularly at the base.

Accompanying species are commonly *Kurzia hippuroides*, *Psiloclada clandestina*, *Ptychomnion aciculare*, *Rhizogonium distichum*, and *Wijkia extenuata*. Other species less often seen with *Bazzania adnexa* are *Acromastigum anisostomum*, *A. colensoanum*, *Bazzania nitida*, *B. novae-zelandiae*, *Dicranoloma dicarpum*, *D. robustum*, *Distichophyllum pulchellum*, *Heteroscyphus billardierei*, *Hypnum chrysogaster*, *H. cupressiforme*, *Lepicolea scolopendra*, *Lepidozia pendulina*, *L. spinosissima*, *Leucobryum candidum*, *Saccogynidium australe*, *Schistochila balfouriana*, *S. nobilis*, *Telaranea tetrapila* and *T. tetradactyla*.

Comments: The apical dentition of the leaves in *Bazzania adnexa* is extremely variable. In well-developed plants it is coarsely denticulate or serrulate not only on the margins of the two or three principal teeth but also on the distal third to half of the lamina. The orientation of the leaves is also variable. Plants often have strongly ventrally secund leaves and, less often, plane and spreading leaves.

The ragged, hyaline distal sector of the underleaf in typical *Bazzania adnexa* may occupy most of the underleaf area. No other New Zealand species of the genus has underleaves of this type. The hyaline portion is composed of thinner-walled, irregularly shaped cells, with an abrupt transition from the hyaline portion of the leaf to the thicker-walled, more collenchymatous quadrate to subrectangular cells of the basal sector (Fig. 94: 10). In recently collected herbarium specimens the margin is colorless and transparent (decolorate) and the central-basal portion of the underleaf is green.

Bazzania semicordata is placed in the synonymy of this species based on Gottsche et al. (1847, p. 720), who described the leaves as "tridenticulatus dentibus inaequalibus interdum minutissimis saepe denticulatus" and the underleaves as reniform and irregularly toothed at

the apex. We have attempted to locate original material of this species, without success, at G, PC, S, STR and W.

Mastigobryum kirkianum Steph. has been placed in the synonymy of *Bazzania hochstetteri* (e.g., Hodgson, 1954). One of us (JJE) has examined the type (G), which is here placed in the synonymy of *B. adnexa*. Type plants have persistent leaves, which may have teeth at the apex and, also, the texture is more like that of *B. adnexa*.

Forms of this species can be difficult to distinguish from other New Zealand *Connatae*, especially *Bazzania hochstetteri* and *B. involuta* var. *submutica*. For details, see the discussion under those taxa. Despite the extreme and often puzzling variability of the species, there is one expression in New Zealand worthy of recognition, the "fo. *aucklandica*" (Lindenberg and Gottsche, 1851), which is here recognized at the varietal level, as follows:

Key to Varieties

1a. Underleaves often distinctly connate, often spreading, quadrate to broadly reniform, plane, the base not dilated, the hyaline cells mostly confined to the distal half; hyaline sector variable, the green thick-walled cells making up as much as half of the underleaf; plants pure green . . . . . var. *adnexa* (p. 430)

1b. Underleaves scarcely connate or free (at least on one side), ± erect, triangular, tapering to a sharply channeled apex (the lateral margins sharply reflexed), the base cordate to subauriculate, with a narrow hyaline margin extending to the insertion; hyaline sector of underleaf often very broad, the green, thick-walled cells few and restricted to the median basal area; plants deep green . . . . . var. *aucklandica* (p. 431)

Bazzania adnexa (Lehm. & Lindenb.) Trevis. var. ***adnexa***

[Fig. 94: 1–6, 9, 10]

Plants pure green; first branch underleaf typically connate to an underleaf of the main shoot, transversely inserted on the stem; flagelliform branches abundantly produced; underleaves connate on both sides, often distinctly so, erect to spreading, broadly reniform, with a ragged, hyaline apex, the lateral margins straight to moderately ampliate (not distinctly cordate at the base), the hyaline portion confined to the distal portion of the underleaf and not extending to the insertion as a narrow border.

Distribution and Ecology: New Zealand: Auckland Islands; Australia: Tasmania, Victoria, New South Wales.

This is one of our most common hepatics, occurring throughout New Zealand, and like other semi-weedy taxa, tolerates a variety of conditions. For example, it occurs in wet, rich forests grading to relatively dry forests and from sea level to the upper reaches of the forest zone, but does not extend into the penalpine or alpine zone. It tolerates a range of exposures from deeply shaded to fully exposed and a variety of substrates, being typically terricolous or corticolous or exceptionally saxicolous (including granite and limestone).

Bazzania adnexa var. ***aucklandica*** (Lindenb. & Gottsche) J.J.Engel & Merrill

[Fig. 94: 7, 8]

Mastigobryum novae-hollandiae f. γ 2 *aucklandicum* Lindenb. & Gottsche, Sp. Hepat. fasc. 8–11: 33, 46. 1851 ("*Aucklandica*"). *Bazzania adnexa* fo. *aucklandica* (Lindenb. & Gottsche) E.A.Hodgs. *ex* Hamlin, Rec. Domin. Mus. 7: 251. 1972. *Bazzania adnexa* var. *aucklandica* (Lindenb. & Gottsche) J.J.Engel & Merrill, Bryologist 97: 319. 1994. Type: Auckland Is., *Hooker* (S!, herb. Lehmann, STR!).

Plants rich, deep green in color, the underleaves appearing small and the stem narrow for plant size; first branch underleaf often free, obliquely inserted, often at right angles to underleaf of main shoot; flagelliform branches sparingly produced; leaves widely spreading and plane; underleaves narrowly connate or free (at least on one side), triangular-cordate, with a channeled apex formed by the sharply reflexed lateral margins, the base cordate to subauriculate, bordered by a narrow hyaline strip extending to the insertion.

Distribution and Ecology: Apparently confined to New Zealand including the Auckland Islands.

Variety *aucklandica* typically occurs on rotted logs and tree-fern bases in forests (120–915 m).

Bazzania hochstetteri (Reicht.) E.A.Hodgs.

[Fig. 97]

Mastigobryum hochstetteri Reicht., Verh. K.K. Zool.-Bot. Ges. Wien 16 (III): 959. 1866. *Bazzania hochstetteri* (Reicht.) E.A.Hodgs., Trans. Roy. Soc. New Zealand 82: 11. 1954. Type: New Zealand, "An alten Stämmen in Wäldern um Coromandel," *Hochstetter*, ex herb. Reichardt (G!).

Mastigobryum mittenii Steph., Hedwigia 25: 241, 242. 1886, *ut nom. nov. pro Mastigobryum affine* Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 147. 1854, *non M. affine* Lindenb. & Gottsche *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 720. 1847 (Mexico). *Bazzania mitteniana* (Steph.) Steph., Hedwigia 28: 132. 1889. Type: New Zealand, North Is., Tararua and Tehawera Mtns., *Colenso*.

Mastigobryum concinnatum Colenso, Trans. & Proc. New Zealand Inst. 18: 245. 1886. Type: New Zealand, North Is., Waipawa Co., near Norsewood, 1885, *Colenso*.

Mastigobryum quadratum Colenso, Trans. & Proc. New Zealand Inst. 18: 246. 1886. *Bazzania quadrata* (Colenso) W.Martin & E.A.Hodgs. *in* W.Martin, Trans. & Proc. Roy. Soc. New Zealand 78: 499. 1950. Type: New Zealand, North Is., Waipawa Co., near Norsewood, 1885, *Colenso 1399* (G!).

Mastigobryum similis Colenso, Trans. & Proc. New Zealand Inst. 18: 247. 1886. Type: New Zealand, North Is., Waipawa Co., near Norsewood, 1885, *Colenso*.

Mastigobryum imbricatistipulum Colenso, Trans. & Proc. New Zealand Inst. 19: 290. 1887 (1886). Type: New Zealand, North Is., Waipawa Co., near Norsewood, 1886, *Colenso*.

Mastigobryum pusillum Colenso, Trans. & Proc. New Zealand Inst. 19: 290. 1887 (1886). Type: New Zealand, North Is., Waipawa Co., near Norsewood, 1886, *Colenso a. 1410* (BM!, G!).

Mastigobryum heterophyllum Colenso, Trans. & Proc. New Zealand Inst. 19: 191. 1887 (1886). Type: New Zealand, North Is., Waipawa Co., near Norsewood, 1886, *Colenso*.

Plants fragile, strongly anisophyllous, prostrate, light green; shoots small, to 1.8(3.9) mm wide. Branching pseudo-dichotomous, of *Frullania* type, widely spreading; branch half-leaf ± symmetric, narrowly ovate, undivided, tapering to a sharp, slender apex; first branch underleaf 2-lobed (rarely bidentate or undivided), transversely to obliquely inserted on main axis

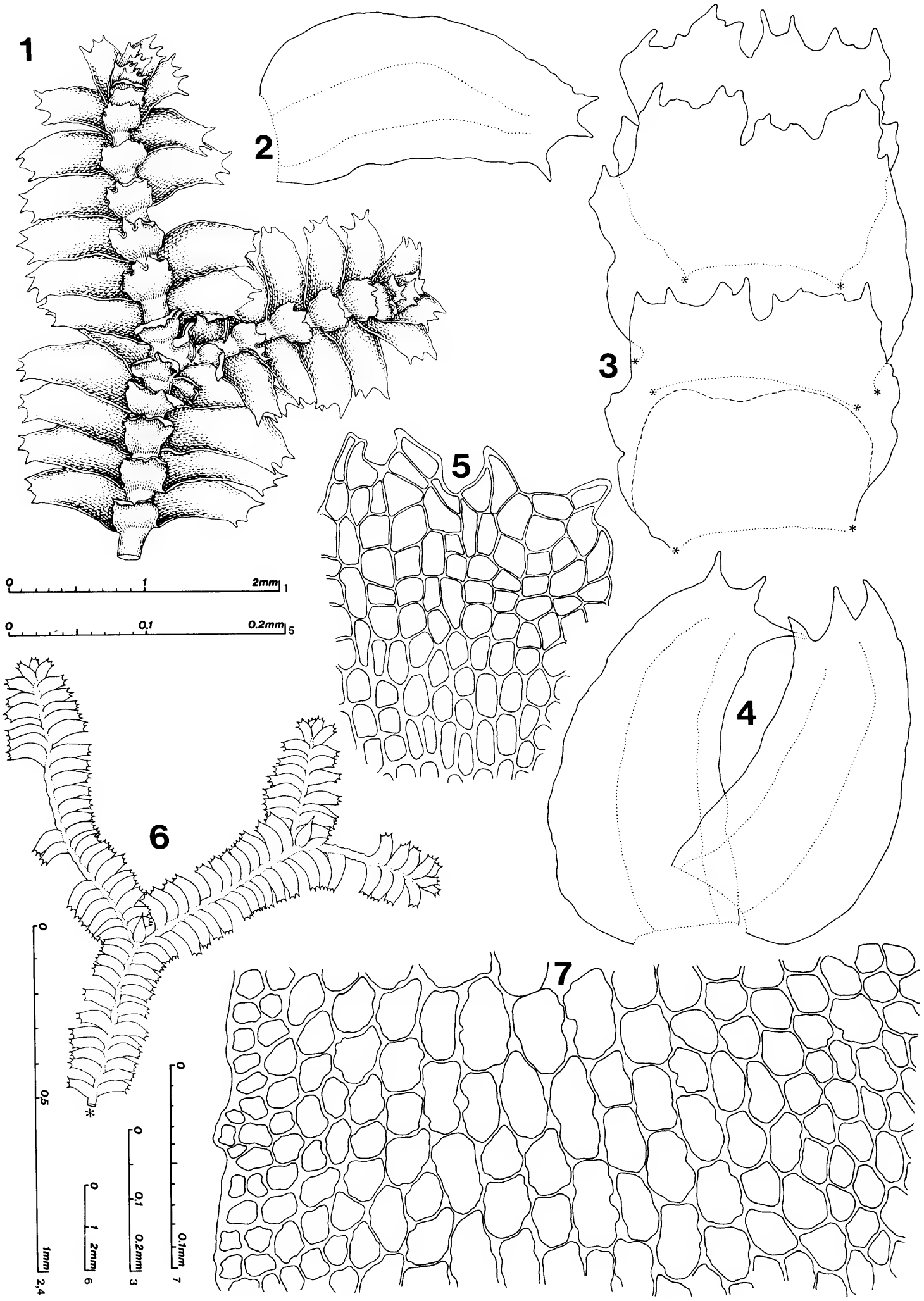

Fig. 97.
Bazzania hochstetteri (Reicht.) E.A.Hodgs. 1. Main shoot, ventral view. 2, 4. Leaf outlines with subvittae indicated. 3. Underleaf outlines, dashed line in lowermost underleaf indicates boundary of hyaline distal sector. 5. Distal portion of underleaf showing cellular detail. 6. Shoot, dorsal view (note branching, missing leaves, and 2 half-leaves). 7. Median sector of leaf showing subvitta. (All from *Child 1985*, New Zealand, North Is., Northland EP, Waipoua Falls [F].)

below base of branch and often basally connate to an underleaf of the main shoot. Ventral-intercalary leafy branches occasionally produced; stoloniform branches occasional. Stems ± slender, the cortical cells moderately thick-walled. Leaves caducous and easily detached, subopposite to opposite, horizontal, contiguous to loosely imbricate, with much of stem exposed in dorsal aspect, widely spreading (ca. 90°); leaves not vittate, 390–600(750) μm wide × 815–1020(1750) μm long, the insertion narrow and distinctly incubous, asymmetrically (and often rather narrowly) ovate-ligulate, subfalcate, the apex moderately to strongly oblique, symmetrically and rather deeply 3-dentate (or predominantly 2-dentate in weaker shoots), the teeth divergent, the ventral tooth often ventrally displaced; teeth 3–5 cells wide at base, narrowly acute, at times subacuminate, terminating in a uniseriate row of 2–3 cells, the terminal cell tapering to a sharp, thick-walled point, the leaf apex otherwise normally entire, sporadically with a few small teeth; dorsal margin ampliate, distinctly arched, at most extending to middle of stem, cordate at base, the margin normally entire, rarely with 1–2 indistinct teeth in distal sector; ventral margin straight to curved gently inward, entire. Cells of leaf differentiated into a broad, diffuse band of enlarged rectangular cells in the median longitudinal portion of the leaf (subvittate), 14–23 μm wide × 26–39 μm long; cells smaller, subquadrate and evenly thick-walled near the margins, particularly the dorsal; median cells 11–19 μm wide × 14–24 μm long, thin-walled, trigones ± knot-like in subvitta cells; cells of leaf base enlarged, the basal cell row of detached leaves often remaining on stem; surface of leaf margin and apex finely papillose. Oil-bodies occupying a conspicuous portion of cell lumen, dull opaque, with a cloud-like appearance, 2–3(4) to (2)3–5 per median leaf cell, 3–5 per cell in subvitta cells, potato-shaped, ovoid to broadly elliptic, often irregularly so to at times sausage-shaped, homogeneous or very coarsely segmented (with up to ca. 3 segments), the oil-body contents often not consistent throughout and appearing to possess some surface texturing, e.g., folds, indentations or strong surface constrictions; oil-bodies 6–8(11) per basal cell, of the same size and texture as at midleaf; oil-bodies at leaf margins 2–3 per cell, of the same size and texture as midleaf or smaller. Underleaves small, spreading, little wider than the stem, connate with the leaves on both sides (or sporadically free on 1 or both sides), quadrate to subrectangular and somewhat narrowed to the insertion, the apex irregularly dentate-lobulate and hyaline (decolorate), with irregular, sharp, often crowded, sinuate teeth (rarely subentire), the hyaline distal sector variable in width, occupying as much as 0.5 of underleaf, composed of thin-walled, sinuate-rhomboidal cells; lateral margins straight, the hyaline cells often extending as a narrow border part way to the insertion; median non-hyaline cells quadrate to ± elongate; surface of hyaline cells finely papillose. Asexual reproduction by caducous leaves. Fungal partner absent.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (20–30 m), South Island (10–600 m), North Island (300–670 m), Chatham Islands (80–260 m). In New Zealand known from Otago (Otago Peninsula), Westland (Stockton, Maimai, Greymouth, Harihari, Okarito), Volcanic Plateau (Rotorua, Atiamuri), Gisborne (Wairoa, Urewera), Auckland (Great Barrier Island, Kaimai Ra.) and Northland (Waipoua Forest) EPs.

A lowland forest plant, on caudices of tree ferns (*Dicksonia fibrosa*, *D. squarrosa*, *Cyathea dealbata* and *C. smithii*), sometimes on tree trunks (recorded from trunks of *Weinmannia racemosa*, *Libocedrus bidwillii* and *Dracophyllum arboreum*), tree stumps, rotten logs and soil, particularly soil banks above streams. It exceptionally occurs on rock; at the headwaters of Poupou Stream (Kaimai Ra., 400–425 m) it grows on bedrock in an open area ca. 10 m above stream level.

Where epiphytic it is found with *Bazzania nitida*, *Calomnion complanatum*, *Dicranoloma menziesii*, *Lopidium concinnum*, *Trichomanes venosum*, *Tylimanthus diversifolius* and *Rhizogonium pennatum*. Where terrestrial it is associated with *Acromastigum colensoanum*, *Balantiopsis convexiuscula*, *Bazzania nitida*, *B. tayloriana*, *Campylopus clavatus*, *Kurzia hippuroides*, *Lepidozia bisbifida*, *Leucobryum candidum*, *Podomitrium phyllanthus*, *Rhizogonium pennatum*, *Riccardia crassa*, *Saccogynidium australe*, *Telaranea herzogii*, *Zoopsis argentea*, *Z. leitgebiana* and *Z. setulosa*.

Comments: Plants of this species have a distinctive aspect, with rather narrow, falcate, contiguous to loosely imbricate leaves, leaving most of the dorsal surface of the stem exposed (Fig. 97: 6). Although clearly related to *Bazzania adnexa*, it differs primarily by its smaller size, fragile texture and easily detached, caducous leaves (Fig. 97: 6). Both species have hyaline-margined underleaves and first branch underleaves that are normally connate to an underleaf of the main shoot. The leaf lamina and the margins of the principal teeth of *B. hochstetteri* are nearly always entire. Weakly developed shoots often have predominantly bidentate leaves. This species is easily distinguished from *B. nova* (which is similar in size and is also caducous-leaved) by the form and areolation of the underleaves, which in *B. hochstetteri* are not dissected into distinct lobes and have a hyaline distal sector made up of thin-walled, colorless cells.

This species was erroneously included with the vittate species of *Bazzania* in a published key to that group (Engel and Schuster, 1988).

Bazzania okaritana Meagher & Glenny

[Fig. 96: 3, 4, oil-bodies, p. 428]

Bazzania okaritana Meagher & Glenny, J. Bryol. 29: 60. *f. 1*. 2007. Holotype: New Zealand, South Is., Whataroa ER, Okarito, Kahuamarua Bluff, S end, 21 Sept. 1994, *Glenny 9191* (CHR); isotypes: (F, MELU).

Plants delicate, strongly anisophyllous, loosely creeping, pale olive-green, shoots medium, to 3.2 mm wide. Branching frequent, pseudo-dichotomous, with *Frullania*-type branches common and rather narrowly spreading, occasionally becoming flagelliform; branch half-leaf symmetric, narrowly ovate, undivided, tapering to an acute apex; first branch underleaf weakly to often strongly asymmetrically bilobed, with one lobe often much longer than the other, the first branch underleaf inserted close to the adjacent main shoot underleaf and at times weakly connate with it. Ventral-intercalary leafy branches sporadic; stoloniform branches occasional, long and whip-like, colorless. Leaves persistent, opposite, horizontal, widely spreading, contiguous to weakly imbricate, with moderate amount of stem exposed in dorsal aspect, widely spreading (ca. 90°); leaves nonvittate, 500–700 μm wide × 1500–1800 μm long, the insertion broad and distinctly incubous, the leaves asymmetrically rather narrowly oblong, the apex truncate to oblique, deeply 3(rarely 2)-dentate, the teeth divergent, weakly to moderately asymmetric, at times with an accessory smaller tooth on the distal sector of the ventral margin; teeth acute to subacuminate, terminating in a uniseriate row of 2–3 cells, the terminal cell tapering to a narrowly rounded to rather sharp, thick-walled summit, the leaf apex otherwise normally entire; dorsal margin moderately ampliate, moderately to rather strongly arched, at most extending to middle of stem, not or at most feebly cordate at base, the margin entire; ventral margin straight to curved gently inward, entire. Cells of leaf differentiated into a broad band comprised of enlarged cells in the median longitudinal portion of the leaf (subvittate), the subvitta occupying a large portion of leaf width; cells smaller and subquadrate near the margins;

median cells subisodiametric to moderately elongated, 25–35 μm wide × 38–49 μm long, thin-walled, with trigones medium and straight-sided to weakly bulging, rather inconspicuous, the cells surrounded mostly by the thin cell walls, the trigones similarly developed or somewhat smaller near the margins and at the leaf apex; surface smooth. Oil-bodies opaque grey, with some glistening, 5–6 per median cell, 2–4 in marginal and submarginal cells of dorsal median sector of leaf, 5–9 per median basal cell, smooth and homogeneous or coarsely segmented (with to 3 segments), potato-shaped and with common pits and creases. Underleaves widely spreading, 1.6–1.9× stem width, narrowly connate with the leaves on both sides, quadrate to subquadrate, moderately narrowing to point of attachment with leaves, the apex entire-repand, at times with 4 broadly rounded feeble projections separated by markedly shallow, lunate "sinuses" (or with 3 weak rounded projections and a variably shaped but distinct lobule), at times truncate and with 4–5 slime papillae at some distance from one another (each marking the position of a repressed lobule) and without the suggestion of a sinus, the apex exceptionally with 2–3 lobuliform processes each terminating in a slime papilla; apex hyaline and decolorate in distal ca. 0.25 or a little less, with this sector comprised of subisodiametric cells, the cells in basal ca. 0.75 up to ca. 2:1 and chlorophyllose; margins of disc entire, often repand, occasionally with a tooth or lobule in distal half; cells different from those of leaves, firm-walled throughout underleaf, with trigones lacking or at most small to medium to (sporadically) weakly bulging; surface of hyaline cells finely papillose. Asexual reproduction lacking.

Androecia and gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (10–350 m). Known from two sites, the type locality in Westland EP and from Fiordland EP, in the Light River, near Lake Dale, 351 m, under *Nothofagus menziesii* forest on a hillslope, in a bouldery area, terrestrial with *Hymenophyton leptopodum* and *Telaranea tuberifera* (CHR 581358). At the type locality it grows on coarse gravels of compacted moraine till, on the back wall of an overhang almost facing the sea that is well protected from weather by hanging vegetation that forms a curtain at the front of the overhang. Surrounding vegetation is stunted coastal scrub.

Comments: *Bazzania okaritana* is most like *B. exempta*, but differs in the frequent development of terminal branches, the persistent leaves, underleaves that are connate on both sides, the finely papillose surface of underleaf hyaline cells, the stronger trigones of subvitta cells, and the suppressed development of lobules at the underleaf apex. Moreover, the dorsal margin of the leaf in *B. okaritana* is not or at most weakly cordate at the base, with the opposing leaves not closely juxtaposed vs. subcordate at the base, with the dorsal bases of opposing leaves closely juxtaposed and appearing (but not actually) connate dorsally (see Fig. 105: 2).

Terminal branches in *Bazzania okaritana* at times may become flagelliform and microphyllous, an unusual feature for the genus.

Underleaf lobules are present in both *Bazzania okaritana* and *B. exempta*, but are far more developed in the latter species (see Fig. 105: 5, 10–14; Fig. 106: 4). The underleaf apex in *B. okaritana* at times may have 4 broadly rounded feeble projections separated by markedly shallow, lunate "sinuses," and in such cases appear rather like weaker lobule development in *B. exempta*. The underleaf apex may develop 3 weak, rounded projections and a variably shaped (but distinct) lobule or, exceptionally, may have 2–3 lobuliform processes of variable shape. In all cases the lobuliform as well as the low rounded processes each terminate in a slime papilla. Underleaves are often truncate, without the suggestion of a sinus, and have 4–5 slime papillae at some distance from one another, each marking the position of a repressed lobule. These are quite unlike the typical underleaves found in *B. exempta*.

Bazzania novae-zelandiae (Mitt.) Besch. & C.Massal.

[Plate 7E, F; Fig. 98; Fig. 100: 1, 2, oil-bodies, p. 441]

Mastigobryum novae-zelandiae Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 148. 1854. *Bazzania novae-zelandiae* (Mitt.) Besch. & C.Massal., Miss. Sci. Cape Horn 5: 233. 1889. Type: New Zealand, North Is., Tehawera and Tararua, *Colenso*.

Mastigobryum spectabile Steph., Sp. Hepat. 3: 455. 1908. Type: New Zealand, Great Barrier Is., *Kirk 48 – c. per.* (G!).

Plants large and robust, suberect to erect in loose cushions or in sprawling mats, deep green to brownish green, rarely gold-brown in life; shoots to 6.5 mm wide. Branching repeatedly and pseudo-dichotomously furcate, *Frullania* type, widely spreading; branch half-leaf ± symmetric, ovate, undivided, tapering to a sharp apex; first branch underleaf undivided or sometimes 2–3-lobed, obliquely to ± longitudinally inserted on ventral or ventral-lateral side of main axis at base of branch or somewhat below it, closely associated with but not connate to an underleaf of main axis. Ventral-intercalary leafy branches sporadically produced, mimicking the terminal branches; stoloniform branches abundantly produced, often very long. Stems wiry, the cortical cells firm, with evenly thickened walls, small, ca. 24–31 μm wide × 55–64 μm long. Leaves opposite, usually ventrally deflexed, weakly to distinctly imbricate, with little or none of stem exposed in dorsal aspect, widely spreading (ca. 90°); leaves not vittate, 1050–1435 μm wide × 2100–2790 μm long, distinctly incubous, asymmetrically narrowly ovate, subfalcate, tapering to a slender truncate apex, the truncation square, the apex coarsely and ± symmetrically (2)3-dentate, plane, the teeth acute to subacuminate, 5–9(10) cells wide at base, terminating in a single cell or uniseriate row of 2 cells, the apex otherwise quite entire; dorsal margin strongly ampliate, distinctly arched, cordate, extending to middle of stem and beyond, entire, not decurrent; ventral margin nearly straight, somewhat dilated to subcordate at extreme base, entire. Cells of leaf ± uniform in size and shape throughout (not subvittate); median cells 24–34 μm wide × 30–44 μm long, somewhat smaller at the apex and much smaller near the margins, especially the dorsal margin; cells thin-walled, with bulging trigones; surface smooth. Oil-bodies occupying a small portion of cell, very pale grey, glistening, in median sector of leaf 4–10 per cell, homogeneous, smooth or slightly textured on surface like a potato, ellipsoid to potato-shaped; acroscopic marginal and submarginal cells with 2–3 per cell, ellipsoidal with rounded ends, 4.5 × 5 μm to 5–6 × 10 μm; basal cells with 6–11 per cell and the same shape and size as at midleaf. Underleaves conspicuous, firm, spreading, plane to slightly concave, subauriculate at base and connate with the leaves on both sides, short-elliptic to subrectangular to lingulate, longer than broad, sometimes with a median sulcus, the apex often truncate, irregularly crenate or occasionally with thin-walled, hyaline, irregular teeth, the apex and often margins with a narrow, ± regular, hyaline (decolorate) border (1–3 cells wide); median cells quadrate to ± elongate, resembling those of the leaves; surface smooth.

Androecia not seen. Perianth (type of *Mastigobryum spectabile*) prominent, rather straight, fusiform, the basal 0.8 with ca. 5 broad plicae and intervening shallow sulci, the perianth gradually narrowing to the contracted mouth, the plicate distally numerous and deep, the mouth irregularly crenate-denticulate by thin-walled, elongate cells that are partially free at their rounded summit.

Distribution and Ecology: New Zealand: Stewart Island (20–530 m), South Island (15–840 m), North Island (60–910 m), Chatham Islands; Australia: Tasmania. In New Zealand known from

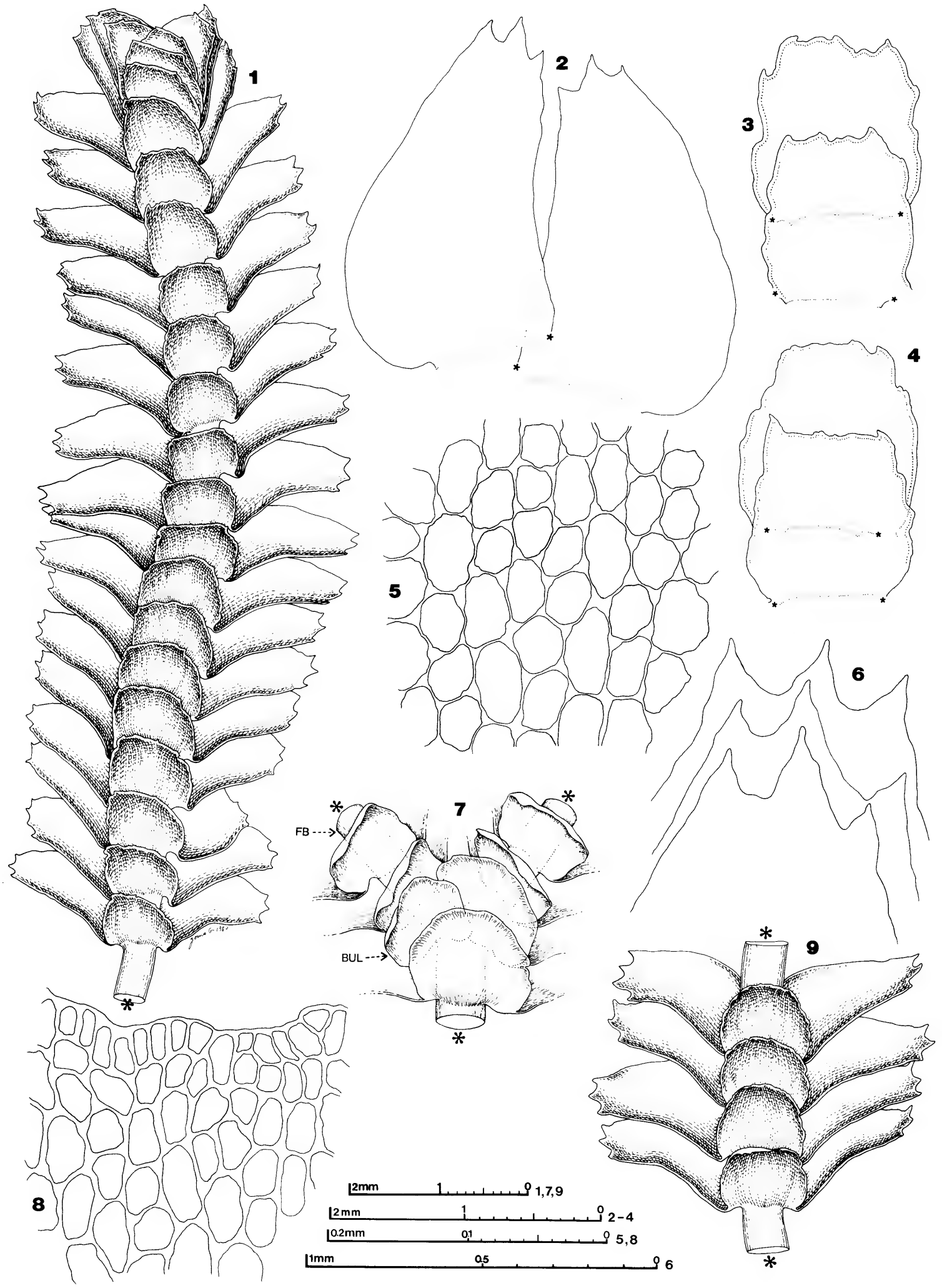

Fig. 98.
Bazzania novae-zelandiae (Mitt.) Besch. & C.Massal. 1. Shoot, ventral view. 2. Leaves (flattened). 3, 4. Underleaves; stipple indicates extent of border of thin-walled, hyaline cells. 5. Median leaf cells. 6. Leaf apices. 7. Juncture of branch and main shoot; note position of first branch underleaf (= BUL; FB = *Frullania*-type branch). 8. Distal sector of underleaf. 9. Portion of shoot, ventral view. (All from *Child 1984*, New Zealand, North Is., Northland EP, track to Tane Mahuta [F].)

Rakiura (Stewart, Whenua Hou, Muttonbird islands), Fiordland, Westland, Western Nelson (Rapahoe Ra. to Karamea), Southern North Island (Orongorongo Valley, Tararua and Ruahine ranges), Taranaki (Mt. Taranaki), Gisborne (Urewera), Auckland (Coromandel Peninsula, Waitakere Ra., Great Barrier and Little Barrier islands) and Northland (Waipoua Forest) EPs.

For the most part a species of forests under high rainfall; the forests are of *Nothofagus*, *Weinmannia*, mixed tall podocarps and *Agathis australis* and plants are mostly found on well-drained substrates like rotten logs and tree bases. It is found on the forest floor in the bryophyte-rich lowland forests of the Jackson River area (south Westland) and is also a floor plant in open forests of *Nothofagus fusca* and *Dacrydium cupressinum* with sparse understory of *Pseudowintera colorata*, *Quintinia serrata* and *Dracophyllum traversii* (Pororari River, Paparoa Natl. Park).

It also occurs over organic substrates, such as bryophyte-covered logs (where it may form large pure patches), rotted tree trunks and stumps as well as tree bases and exposed roots. On Mt. Te Aroha (880–890 m) plants occurred as scattered patches on the floor of a steep slope in a forest dominated by stunted *Nothofagus menziesii*, associated with *Dracophyllum* and *Quintinia serrata*. On Mt. Moehau (Coromandel Forest Park, ca. 800–840 m) plants formed dense mats over the roots and lower tree trunk on a vertical bank in an area of rocky outcrops and shrub-heath communities including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus* and *Corokia buddleioides*.

On Stewart Island, for example, at Fern Gully Track (20–30 m) plants occurred in *Fuchsia excorticata – Griselinia littoralis* forest with a *Blechnum discolor* ground tier; at the site the species formed a large, raised colony over very thick humus on the forest floor. Also on Mt. Rocky Track (390–475 m) under an overhang of tussock blades near a narrow stream in a stunted and dense *Leptospermum scoparium – Dracophyllum – Weinmannia racemosa* forest to 3–4 m tall. On Pryse Peak (350–355 m) plants formed small, golden brown cushions in an open shrubland consisting of *Leptospermum scoparium*, *Olearia colensoi*, *Gahnia* and emergent *Podocarpus hallii*.

In south Westland, Fiordland and Stewart Island it is occasionally epiphytic.

The most common accompanying species are *Heteroscyphus billardierei*, *Hypnum cupressiforme* and *Leucobryum candidum*, *Rhizogonium pennatum* and *Wijkia extenuata*. Other species found with *Bazzania novae-zelandiae* are *B. adnexa*, *Dicranoloma robustum*, *Hymenophyllum multifidum*, *Hypnodendron comosum*, *Lepicolea scolopendra*, *Lepidozia pendulina*, *L. ulothrix*, *Plagiochila ramosissima*, *P. retrospectans*, *Rhizogonium distichum*, *Riccardia cochleata*, *R. crassa*, *Schistochila glaucescens*, *Telaranea tetrapila* and *Weymouthia cochlearifolia*.

Comments: This species has truncate, subentire underleaves, which are elliptic to subrectangular in outline and longer than broad (Fig. 98: 1, 3, 4, 9). The apex lacks a ragged, hyaline margin (or only the marginal row of cells is hyaline; Fig. 98: 3, 4). The leaf areolation is ± uniform throughout and not at all subvittate. The leaf apex and margins of lamina are quite entire and the principal teeth broadly triangular (Fig. 98: 6). No other New Zealand member of the genus approaches *Bazzania novae-zelandiae* in stature. The leaves of *B. involuta* and *B. adnexa*, the two species closest in size, are at most 1.4 and 1.9 mm long, respectively, while those of *B. novae-zelandiae* are at least 2.1 mm long.

Bazzania nova J.J.Engel & Merrill

[Fig. 99; Fig. 100: 3, oil-bodies, p. 441]

Bazzania nova J.J.Engel & Merrill, Bryologist 97: 313. *f. 1*. 1994. Holotype: New Zealand, South Is., Westland Prov., Waikukupa River, S of Waiho River, ca. 500 ft., *Child H4926* (F); isotype: (CHR).

Plants strongly anisophyllous, prostrate, light green; shoots small, to 2.6 mm wide. Branching pseudo-dichotomous, of *Frullania* type, widely spreading; branch half-leaf ± symmetric, narrowly ovate, undivided, tapering to a sharp apex; first branch underleaf (2)3-lobed, with accessory teeth on margin of disc, free, obliquely inserted on ventral-lateral side of main axis somewhat below base of branch. Ventral-intercalary leafy branches rarely produced; stoloniform branches sporadically produced. Stems ± slender, the cortical cells moderately thick-walled. Leaves caducous, subopposite, horizontal, loosely imbricate, with much of stem exposed in dorsal aspect, widely spreading (ca. 90°); leaves not vittate, 400–560(615) μm wide × 685–880(945) μm long, distinctly incubous, asymmetrically ovate-ligulate, straight or subfalcate; apex moderately to strongly oblique, asymmetrically 3-dentate, the ventral tooth often strongly ventrally displaced, the teeth 2–4(6) cells wide at base, narrowly to broadly acute, at times apiculate, terminating in a single cell or a uniseriate row of 2–3 cells, the terminal cell tapering to a rounded, thick-walled point, the leaf apex otherwise entire; dorsal margin ampliate, distinctly arched but usually not extending to middle of stem, cordate at base, the margin entire; ventral margin straight, entire or sparingly and irregularly denticulate. Cells of leaf differentiated into a broad band of enlarged rectangular cells in the median longitudinal portion of the leaf (subvittate), the subvitta occupying most of leaf width in smaller leaves; cells smaller and subquadrate near the margins; median cells 24–34 μm wide × 26–38(48) μm long, thin-walled, trigones ± knot-like in all leaf cells, the free wall also strongly thickened; surface smooth or the teeth finely papillose. Oil-bodies in subvitta (3)4–6(10) per cell, colorless, homogeneous and smooth or coarsely granular on surface due to surface restrictions, crescentic with parallel sides and rounded ends, less often ellipsoidal, 7–10 × 9–24 μm; at midleaf near margin, 2–3 per cell, smooth or coarsely lumpy, 6 × 8–16 μm; intramarginal row of cells with only (1)2 oil-bodies per cell. Underleaves firm, erect to widely spreading, connate on both sides, quadrate to cuneate to subrectangular, broader than long, the apex ± regularly to irregularly 4–6-lobed to ca. 0.3, the lobes rigid, somewhat divergent, often reflexed, slenderly acuminate to spiniform, at times truncate, entire or variously armed with a divergent spur, the lobe then appearing bent, truncate, hook-like, or twisted, the lobes ultimately terminating in a uniseriate row of 2–4 cells, the terminal cell tapering to a thick-walled point; margins of disc with a single tooth, or the accessory teeth lobuliform, the underleaf then appearing 6–8-lobed; no hyaline cells present; cells with trigones as in leaves; surface minutely papillose on tips of lobes.

Asexual reproduction by caducous leaves and regeneration from leaves.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (35–1200 m), North Island (1310 m). Known from Westland (Waikukupa River, Haupiri River, Reefton), Western Nelson (Little Wanganui River, Lead Hills) and Gisborne (Maungawaru Plateau) EPs. Probably more widespread and common than records indicate.

In forests, often along ridgelines, of *Nothofagus truncata*, *Weinmannia racemosa*, *Quintinia serrata*, *Metrosideros umbellata* and *Libocedrus bidwillii*. Epiphytic (recorded on trunks of

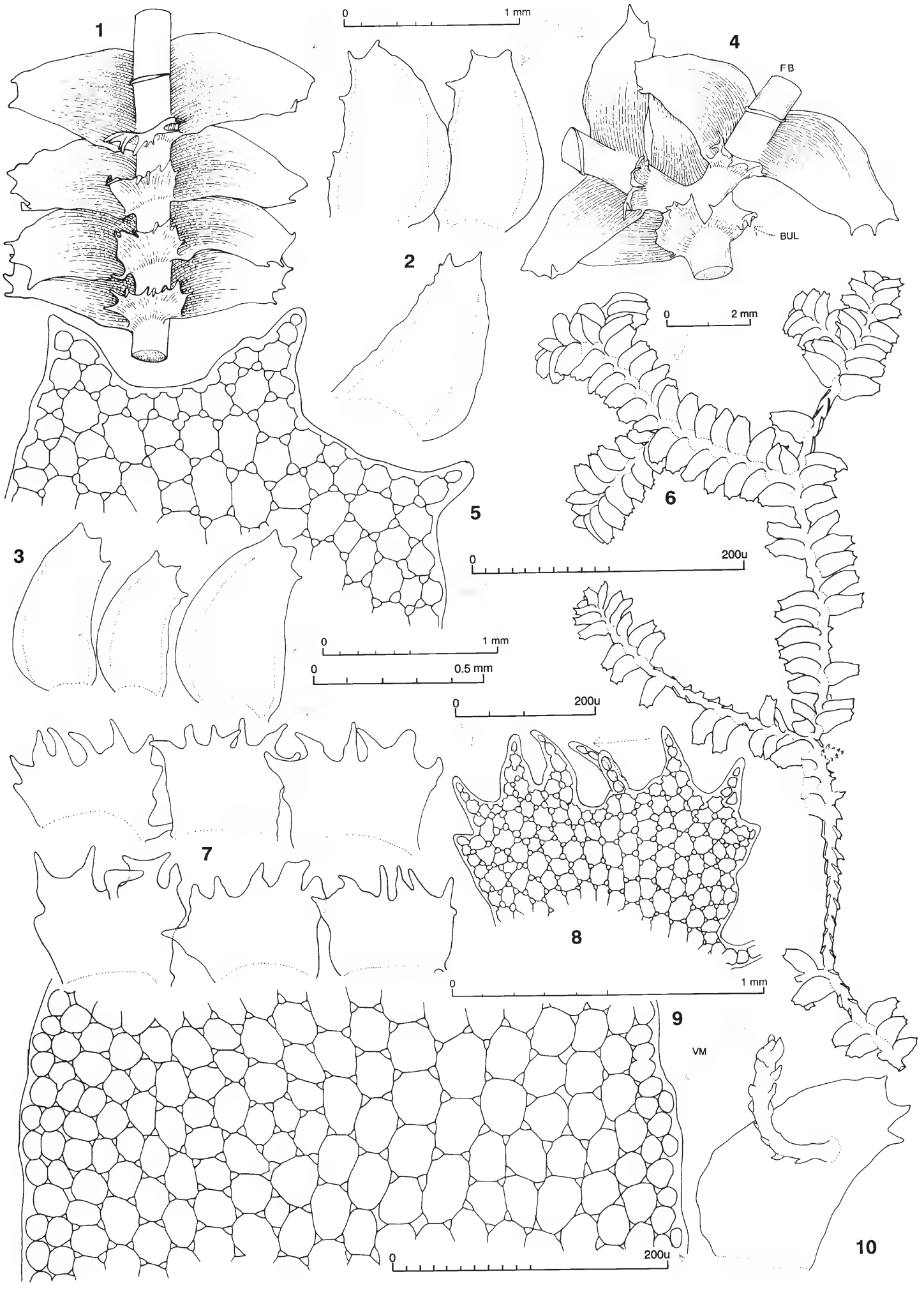

Fig. 99.
Bazzania nova J.J.Engel & Merrill. 1. Sector of leading shoot, ventral view. 2, 3. Leaves. 4. Juncture of branch and main axis, ventral view; note position of first branch underleaf (= BUL; FB = *Frullania*-type branch). 5. Leaf apex. 6. Sector of leading shoot, dorsal view. 7. Underleaves. 8. Underleaf; note spur-like extension of underleaf lobe (at arrow). 9. Median sector of leaf (VM = ventral margin). 10. Regenerant from leaf. (Figs. 1, 3–10, from holotype; 2, from *Druce*, New Zealand, Gisborne EP, Maungawaru Plateau.)

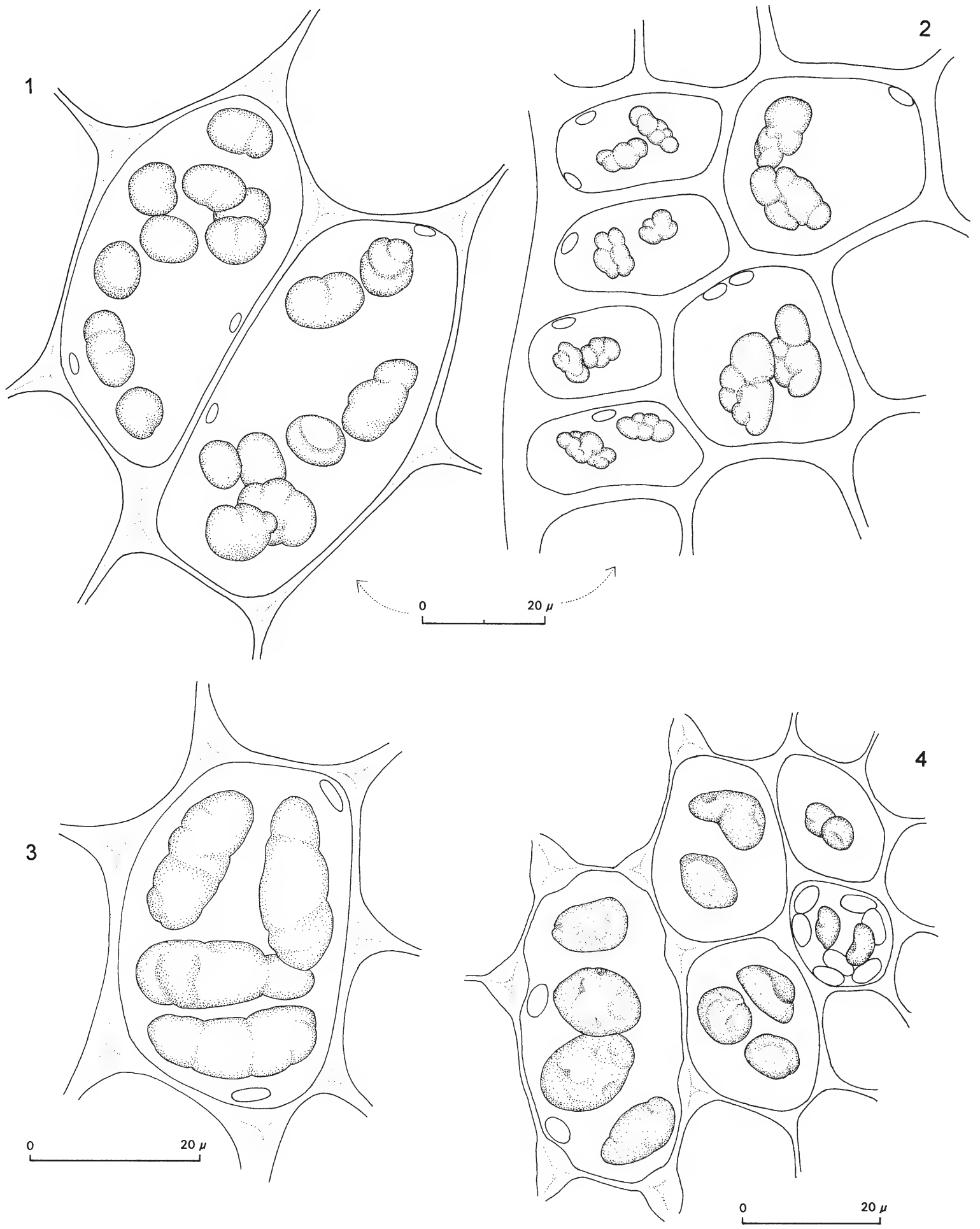

Fig. 100.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Bazzania novae-zelandiae* (Mitt.) Besch. & C.Massal. Cells from median sector of leaf. 2. *Bazzania novae-zelandiae* (Mitt.) Besch. & C.Massal. Marginal and submarginal cells. 3. *Bazzania nova* J.J.Engel & Merrill. Vitta cells. 4. *Bazzania nitida* (F.Weber) Grolle. Vitta cell (left) and non-vitta cells. (Figs. 1, 2, from *Glenny 9175*, New Zealand, South Is., Westland EP, Mt. Te Kinga; 3, from *Glenny 9154*, New Zealand, South Is., Westland EP, Haupiri Ra.; 4, from *Glenny 9176*, New Zealand, South Is., Westland EP, Mt. Te Kinga.)

N. truncata, *Griselinia littoralis*) with *Hymenophyllum flabellatum*, *Plagiochila annotina* and *Rhizogonium pennatum* or on humic soil in damp protected places with *Leucobryum candidum*, *Rhizogonium distichum*, *R. pennatum* and *Zoopsidella caledonica*. Also found on a stump of *Halocarpus biformis* with *Hymenophyllum malingii*.

At Paparoa Natl. Park (Inland Pack Track, ca. 35 m), on bark of *Nothofagus* in an area of limestone outcrops and cliffs in a mixed broadleaf forest with *Nothofagus* and *Leptospermum scoparium*. Also on the Maungawaru Plateau (Raukumara Ra., 1310 m) with *Bazzania monilinervis* and *Leucobryum candidum* (*leg. Druce*, MPN *sub B. monilinervis*).

Comments: The most striking feature of this species is the unique form and texture of the underleaves, which are ± regularly divided into 4–6 slenderly acuminate, rigid lobes (Fig. 99: 7) and are composed entirely of thick-walled cells, with well-developed trigones (Fig. 99: 8). The other nonvittate, opposite-leaved *Bazzania* species in New Zealand have undivided underleaves, with a variously developed hyaline sector composed of leptodermous cells. *Bazzania nidita* and *B. tayloriana* have regularly lobed underleaves that are composed of decolorate cells, entirely or in major part, and have alternate, vittate leaves.

The underleaf lobes of *Bazzania nova* often appear twisted, with the spur-like, lateral projections projecting abaxially, reminiscent of the projecting spines on the underleaf lobes of *Lepidozia setigera*.

Most likely to be confused with *Bazzania hochstetteri* because the leaves of both species are caducous and both are usually epiphytic. The underleaves of *B. nova* differ from those of *B. hochstetteri* in lacking any hyaline cells and in having conspicuously long marginal lobes.

Sect. ***Vittatae*** (Steph.) Fulford

Mastigobryum sect. *Vittata* Steph., Hedwigia 25: 246. 1886.
Bazzania sect. *Vittatae* (Steph.) Fulford, Ann. Cryptog. Phytopathol. 3: 155. 1946.

Bazzania nitida (F.Weber) Grolle

[Fig. 100: 4, oil-bodies, p. 441; Fig. 101]

Jungermannia nitida F.Weber, Hist. Musc. Hepat. Prodr. 43: 1815. *Bazzania nitida* (F.Weber) Grolle, Rev. Bryol. Lichénol. 29: 210. 1960. Type: South Africa, Cape Prov., Cape of Good Hope, *Thunberg* (*non vidi*).

Mastigobryum convexum (Thunb.) Lindenb. *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 215. 1845. *Jungermannia convexa* Thunb., Prodr. Plant. Cap. 173. 1800, *non J. convexa* Scop., Fl. Carniol., ed. 2, 2: 349. 1772. *Bazzania convexa* (Thunb.) Trevis., Mem. Reale Ist. Lombardo III, 4: 414. 1877. Type: South Africa, Cape Prov., Cape of Good Hope, *Thunberg* (*non vidi*).

Mastigobryum fugax Colenso, Trans. & Proc. New Zealand Inst. 18: 247. 1886. Type: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso* (*non vidi*).

Mastigobryum obtusatum Colenso, Trans. & Proc. New Zealand Inst. 19: 287. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso* (*non vidi*).

Mastigobryum fissistipum Steph., Sp. Hepat. 3: 533. 1909. *Bazzania fissistipa* (Steph.) Pearson, Univ. Calif. Publ. Bot. 10: 320. 1923. Lectotype (*nov.*): New Zealand, South Is., Mt. Winterslow, 3000–4000 ft., 27 Mar. 1906, *Beckett 471* (G!). Isolectotype: (CHR 585837 ex herb. Beckett!).

Plants small, prostrate, green to pale yellow-green to olive-green, the vitta often amber at least on dry leaves; plants when dry distinctly nitid and with leaves membranous; shoots to 1.1–1.2 mm wide. Branching rather frequently pseudo-dichotomously furcate, the branches of *Frullania* type, widely spreading, sporadically becoming flagelliform; branch half-leaf ± symmetric, ovate, undivided, nonvittate, tapering to a sharp apex (rarely bidentate); first branch underleaf 3(4)-lobed, transversely inserted on ventral-lateral side of juncture of main axis and branch, free and often distant from underleaf of main axis. Ventral-intercalary branches occasional, leafy and often becoming leading shoots; stoloniform branches sporadically present, rarely reverting to leafy branches. Stem cortical cells very thick-walled. Rhizoids from basal cells of underleaves of main shoot. Leaves alternate, horizontal, contiguous to weakly imbricate, much of stem exposed in dorsal aspect, widely spreading (ca. 90°), plane to moderately convex, the margins and especially the apex narrowly inflexed; leaves vittate, (365)400–530 μm wide × 600–900 μm long, strongly incubous, asymmetrically ovate; apex broadly rounded to often obliquely truncate, with 3 small, often obscure teeth, the teeth typically 2–3 cells wide at base, the entire tooth at times of only 1–2 cells, often not evident in dorsal view due to the strongly deflexed apex, the apex otherwise entire; dorsal margin strongly ampliate, distinctly and broadly arched, subauriculate, extending to middle of stem or somewhat beyond, entire, not decurrent; ventral margin nearly straight, entire, not decurrent. Vittae of leaves distinct, running parallel to and 3–5 cells within the ventral margin at midpoint of leaf, the vitta of 3–4 cell rows; cells of vitta 20–28 μm wide × 23–36 μm long, with large, bulging trigones; cells outside the vitta much smaller, 12–19 μm wide and long, with trigones large and bulging; surface smooth or faintly and indistinctly striolate. Oil-bodies present only in some distal cells of both margins, lacking in the marginal cells below, the oil-bodies lacking in many intramarginal cells but present and 2 per cell in some, the cells in several cell rows acroscopic to the vitta, typically 2 per cell, 2–2.5 × 3–4 μm, and gradually becoming larger toward vitta. Oil-bodies very pale grey, with a cloudy aspect, in vitta cells 2–3 per cell, blood platelet-like (discoid with rounded edges), homogeneous, smooth, but with several depressions and weak folds to lend similarity in texture to a potato, in all parts of vitta 8–9 × 12–13 μm when seen side on. Oil-bodies of non-vitta cells similar to those of the vitta except much smaller and sometimes fewer per cell (1–2). Non-vitta cells densely chlorophyllose, the chloroplasts tightly packed. Underleaves inconspicuous, about as wide as stem, membranous, free or narrowly connate to leaf on one side, appressed to the stem, distant, plane, subquadrate to cuneate, 4-lobed to ca. 0.5; lobes attenuate, 3–4 cells wide at base, entire, terminating in 2 laterally juxtaposed cells or at most a uniseriate row of 2 cells, the lobe summit often with an elongated slime papilla; lobes and distal sector of disc colorless, the cells elongate, moderately thick-walled, the cell walls darkening with age; cells in median basal sector small, isodiametric, thick-walled and densely chlorophyllose, sporadically giving rise to abundant rhizoids; disc margins entire; surface as in leaves.

Androecia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from leading shoots; bracts ventricose-cucullate to canaliculate, 2-lobed to ca. 0.2–0.3, the lobes acute, sometimes apiculate; dorsal margin of disc slightly dilated or with an acute lobule, the basal sector of dorsal margin entire but with a few slime papillae, the distal sector crenulate; antheridia 1 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches issuing from main stem; bracts of innermost series much larger than leaves, erect and closely ensheathing the perianth, the bracts concave, ovate; apices with 4 long-attenuate lobes that terminate in a single cell or a uniseriate row of 3–4 cells, the lobes composed of ± regularly rectangular cells, the apical end of the marginal cells sometimes feebly diverging, the margins at

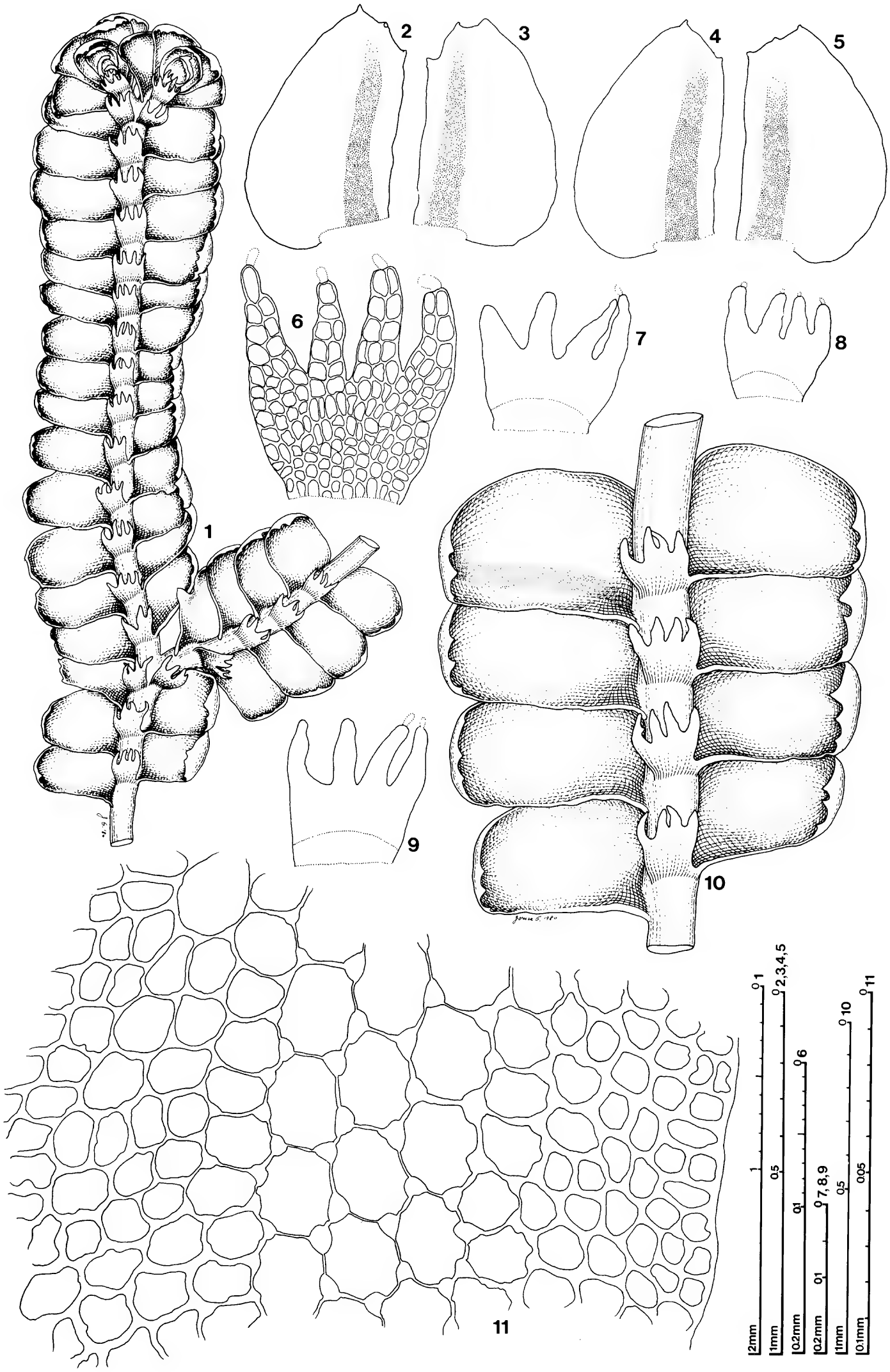

Fig. 101.
Bazzania nitida (F.Weber) Grolle. 1. Axis, ventral view. 2–5. Leaves, with boundary of vitta indicated. 6. Underleaves showing cellular detail. 7–9. Underleaves, stippled area indicates region of small, thick-walled, basal cells. 10. Axis, ventral view. 11. Median leaf cells showing vitta. (Figs.

times with a partially laterally free cell, the lobe margins thus finely and irregularly crenulate; lamina composed of ± regularly short-rectangular cells, the margin bordered by cells of variable shape, most only slightly longer than wide, a few long and narrow, the apical or free end of marginal cells at times divergent and forming a short projection or a tooth, the margin irregularly and sparingly to rather copiously crenate-denticulate, the teeth rarely composed of more than one cell; bracteole similar in size and form. Perianth prominent, straight to curved, fusiform, terete below, becoming somewhat inflated in median sector, the distal half pluriplicate and gradually narrowing to the contracted mouth, the mouth irregularly denticulate-dentate, the processes thin-walled and laterally free for varying lengths, at times half or all of cell laterally free; perianth 1(locally 2)-stratose in basal sector.

Seta seen only in collapsed state. Capsule wall 28–30 μm thick, of 3 layers; outer layer of cells with two-phase development, the longitudinal walls with sinuous, sheet-like thickenings and a few nodule-like swellings alternating with walls that are devoid of thickenings (or are sporadically locally thickened), the transverse walls devoid of thickenings or sporadically with an isolated swelling; innermost layer of cells readily becoming detached, equal to or thicker than intermediate layer, with ± tiered, narrowly and at times irregularly rectangular cells with semiannular bands common, rather wide, usually complete, rarely forked.

Spores and elaters not seen.

Distribution and Ecology: A pan-south-temperate species, occurring in New Zealand, South Africa, southern South America and Brazil. Within New Zealand: Stewart Island (530 m), South Island (0–1070 m), North Island (915–1100 m). Known from Fiordland, Otago, Canterbury, Westland, Western Nelson, Marlborough (Pelorus Valley), Southern North Island (Tararua Ra.), Volcanic Plateau, Gisborne (Wairoa), Taranaki and Auckland EPs. Apparently more common in the South Island than the North Island.

A species occurring at a variety of elevations in wet forests, it is typically found on organic substrates such as bark, tree buttresses, decayed stumps, humus over tree roots especially those of *Metrosideros umbellata*, logs and tree-fern trunks. Occasionally it is epiphytic, on trunks of trees such as *Libocedrus bidwillii*, *Dacrycarpus dacrydioides* and *Weinmannia racemosa*. It may occur on inorganic substrates such as in hollows and cave-like overhangs of cliffs and banks, where it may be a component of pendent sheets of bryophytes, and in such sites it is quite shade tolerant. The species often grows in loosely interwoven pure mats. Commonly associated species are *Bazzania adnexa*, *Kurzia hippuroides*, *Leucobryum candidum*, *Psiloclada clandestina*, *Rhizogonium distichum*, *R. pennatum*, *Wijkia extenuata* and *Zoopsis argentea*. Less commonly it can be found with *Acromastigum anisostomum*, *A. colensoanum*, *Bazzania hochstetteri*, *Categonium nitens*, *Dicranoloma billardierei*, *D. robustum*, *Grammitis billardierei*, *Hymenophyllum revolutum*, *Lepidozia bisbifida*, *L. digitata*, *Leptotheca gaudichaudii*, *Rhaphidorrhynchium amoenum* and *Zoopsis matawaia*.

On Stewart Island found at the summit area of Mt. Rocky where it occurred in a protected, sheltered pocket in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus*.

1, 10, from *Child 1768*, New Zealand, Haast watershed [F]; remainder from *Child 1765*, New Zealand, Haast watershed [F].)

Comments: *Bazzania nitida* is a very distinctive species, due to its strongly convex, "varnished" leaves, which are often dark olive-green, frequently with a sharply contrastingly colored, orange-tinged vitta. The ventral aspect of the plants is also highly characteristic, with underleaves membranous, appressed to the stem and 4-lobed to about half their length (Fig. 101: 6–9).

The name *Bazzania nitida* has now replaced the more familiar name *B. convexa* (Lindenb.) Trevis. (cf. Grolle, 1961d).

Lectotype plants of *Mastigobryum fissistipum* have teeth at the leaf apex obscure and observable only in ventral view. The underleaves are obcuneate and distally ca. 2× the stem width. A Colenso specimen (no. *1715*) without locality at G is probably a syntype.

Bazzania monilinervis (Lehm. & Lindenb.) Trevis.

[Fig. 102; Fig. 104: 4, oil-bodies, p. 452]

Jungermannia monilinervis Lehm. & Lindenb. *in* Lehm., Nov. Min. Cogn. Stirp. Pug. 4: 56. 1832. *Mastigobryum monilinerve* (Lehm. & Lindenb.) Nees *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 223. 1845. *Bazzania monilinervis* (Lehm. & Lindenb.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 414. 1877. Type: Australia.

Plants prostrate, yellow-green to pale olive-green; plants when dry distinctly nitid and with leaves membranous; shoots small, to 2.5 mm wide. Branching rather frequently pseudodichotomously furcate, the branches of *Frullania* type; branch half-leaf ± symmetric, ovate, undivided, nonvittate, tapering to a sharp apex; first branch underleaf 2–3-lobed, inserted on ventral-lateral side of stem below the branch, free. Ventral-intercalary branches occasional, leafy; stoloniform branches sporadically present. Stem cortical cells with thick longitudinal walls, the transverse walls ± thin. Rhizoids from basal cells of underleaves of main shoots. Leaves rigid, alternate, horizontal, imbricate, covering some or most of stem in dorsal aspect, widely spreading (ca. 90°), plane to slightly convex (strongly convex when dry), the apex often slightly deflexed; leaves vittate, 420–565 μm wide × 730–1120 μm long, the insertion narrow and strongly incubous, the leaves asymmetrically narrowly ovate; apex transverse to moderately oblique, symmetrically and rather deeply 3-dentate, the teeth widely divergent, spinulose, 3–4(5) cells wide at base, narrowly acuminate, terminating in a uniseriate row of 4–11 irregularly thick-walled cells, the terminal cell tapering to a rounded tip, the apex otherwise entire; dorsal margin strongly ampliate, extending to middle of stem to across and slightly beyond the stem, cordate to subauriculate at base, entire; ventral margin nearly straight, entire. Vittae of leaves sharply defined, running parallel to and 5–6 cells within the ventral margin and broadening in the apex, the vitta 3–4 cells wide; cells of vitta 25–31 μm wide × 26–39 μm long, very thin-walled, with distinctly knot-like trigones; cells outside the vitta much smaller, 11–18 μm wide and long, ± evenly thick-walled; surface smooth to indistinctly papillose. Oil-bodies present in all leaf cells except cells of the uniseriate row which have only chloroplasts, the cell lumen of both non-vitta and vitta cells packed with oil-bodies and chloroplasts, the oil-bodies in vitta cells nearly filling the lumen, 2–6 (up to 9, perhaps the result of oil-bodies breaking up) per cell, homogeneous, broadly elliptic to ovate, (8.8)10.7–13.7 × 18.5–21.5 μm, the surface appearing lumpy, distorted and potato-like, occasionally having a pinch-like depression, with very irregular internal differentiation of huge oil masses which give an irregularly cloudy appearance to the oil-body. Oil-bodies in nonvittate cells

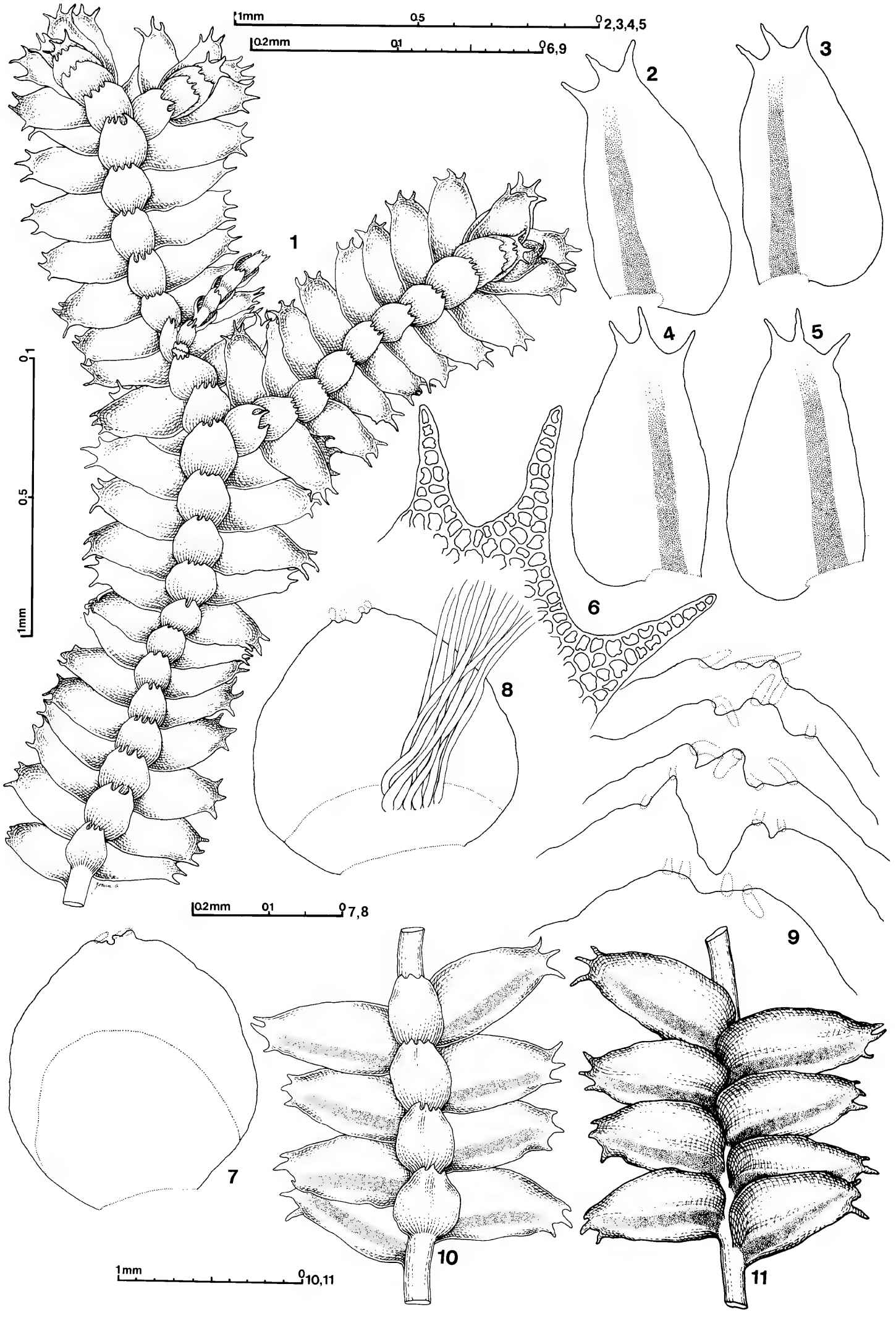

Fig. 102.
Bazzania monilinervis (Lehm. & Lindenb.) Trevis. 1. Shoot, ventral view. 2–5. Leaves, showing position of vitta. 6. Leaf apex. 7, 8. Underleaves, stipple indicates region of smaller, thick-walled cells; note in fig. 8 the rhizoid field. 9. Underleaf apices. 10. Portion of shoot, ventral view. 11. Portion of shoot, dorsal view. (All from *Engel 14858*, Tasmania, King R.)

hyaline, 2(3) per cell, essentially smooth but with faint, irregular, internal oil-droplets, the oil-bodies 2.9–3.9 × 6.8–7.8 μm. Chloroplasts large for cell size. Underleaves conspicuous, ca. 2.5× stem width, membranous, free, appressed to the stem, contiguous to feebly imbricate, slightly convex (ventral view), wide elliptic to wide ovate or ± orbicular, the apex very shallowly divided into 4 small irregular teeth or almost imperceptibly 4-dentate, in either case the teeth terminating in an elongated slime papilla, or the apex truncate and entire except for 4 closely juxtaposed slime papillae; distal ca. 0.5–0.8 of underleaf colorless, the cells ± isodiametric, thin- to slightly and evenly thick-walled; cells in the basal sector thick-walled and densely chlorophyllose, sporadically giving rise to abundant rhizoids; margins entire; surface smooth.

Androecia and gynoecia not seen.

Distribution and Ecology: New Zealand: Stewart Island (10–530 m), South Island (520–850 m), North Island (835–1340 m); Australia: Tasmania (where apparently common), Victoria, New South Wales. Miller et al. (1983) report the species for Tahiti; the record requires confirmation. In New Zealand known from Fiordland, Westland (Whataroa), Western Nelson, Southern North Island (Tararua Ra.), Gisborne (Raukumara Ra.) and Auckland (Coromandel Peninsula) EPs.

The species has a sporadic distribution in New Zealand. On Stewart Island the species occurs between 10 and 340 m within the forest zone and forms loose, often pendent, at times large mats in damp, deeply shaded, protected niches such as in crevices or on ledges beneath overhangs of rocky outcrops, or under partial cover of logs, or at the base of tree trunks. In the South Island known from Westland Natl. Park (Gillespies Beach Road, between Tornado and Whelan creeks) occurring on tree bark with *Acromastigum mooreanum* in a wet forest. On Mt. Turiwhate (central Westland, 850 m) in a root cave under *Metrosideros umbellata* in upper montane *Weinmannia racemosa – Metrosideros umbellata* forest. In the North Island known from Coromandel Forest Park (835 m, summit of Table Mtn.) in a wet mossy forest of *Lepidothamnus intermedius*, *Ixerba brexioides* and *Dacrydium cupressinum* with occasional *Phyllocladus glaucus*. At this site it occurred on a bryophyte-covered stump with *Acromastigum anisostomum* and *A. marginatum* as well as in loose, soft, pendent masses in deeply shaded niches such as from the ventral-lateral side of a shaded bryophyte-covered log. Also on Mt. Te Aroha (880–890 m) forming loosely pendent tufts in deeply shaded, protected niches on banks within a forest dominated by stunted *Nothofagus menziesii*, associated with *Dracophyllum* and *Quintinia serrata*. Also on the Maungawaru Plateau (Raukumara Ra., ca. 1310 m, *Druce s.n.* [MPN]) where corticolous and with *Bazzania nova* and *Leucobryum candidum*. In the Marino Mtns. it occurred on the roof of a cave formed by a sandstone boulder under *Nothofagus menziesii* forest in a site affected by cold, moist air drainage. This is the only New Zealand species of *Bazzania* known to be epiphyllous—on tree ferns (*Cyathea*) with *Radula pseudoscripta* and *Heteroscyphus* sp. on Stewart Island (Tin Ra., West Hut, *Martin 593* [MPN]; Port Pegasus, *Martin 610, 623* [MPN]). Other accompanying species are *Balantiopsis diplophylla*, *Categonium nitens*, *Hymenophyllum flabellatum*, *H. revolutum*, *Lepidozia spinosissima*, *Mittenia plumula*, *Plagiochila fasciculata*, *Psiloclada clandestina*, *Rhizogonium pennatum*, *Telaranea elegans* and *Tylimanthus diversifolius*.

Comments: Readily distinguished by the vittate leaves, the widely divergent spinulose teeth of the leaf apices and the large orbicular underleaves, which are shallowly lobulate or divided into 4 minute teeth terminating in an elongate slime papilla (Fig. 102: 7–9) which is sometimes the only indication of the lobulate nature of the underleaf. The leaves are strongly convex and distinctly membranous (like onion skin in appearance) when dry. The narrowly

acuminate teeth of the leaf apex are unique among New Zealand *Bazzania* species and consist almost entirely of a uniseriate row of up to 11 cells (Fig. 102: 6). Useful field characters that will distinguish the species are the highly nitid texture of the plants, the membranous, vittate leaves and the divergent, acuminate lobes. This species is the only one of our species known to be epiphyllous.

Sect. ***Glaucobazzania*** J.J.Engel

Bazzania sect. *Glaucobazzania* J.J.Engel, Novon 17: 310. 2007. Type: *Bazzania tayloriana* (Mitt.) Kuntze (≡ *Mastigobryum taylorianum* Mitt.)

Bazzania tayloriana (Mitt.) Kuntze

[Plate 8A; Fig. 103; Fig. 104: 1, 2, oil-bodies, p. 452]

Mastigobryum taylorianum Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 147. *pl. 100, f. 5*. 1854. *Bazzania tayloriana* (Mitt.) Kuntze, Revis. Gen. Pl. 2: 832. 1891. Type: New Zealand, North Is., Tehawera, *Colenso*.

Mastigobryum delicatulum Colenso, Trans. & Proc. New Zealand Inst. 18: 246. 1886. Type: New Zealand, Waipawa Co., 1885, *Colenso 1400* (BM!, G!).

Mastigobryum obscurum Colenso, Trans. & Proc. New Zealand Inst. 19: 292. 1887 (1886). Type: New Zealand, Wairoa Co., hill country between Mohaka and Lake Waikara, 1886, *Hamilton*.

Mastigobryum obtusistipulum Colenso, Trans. & Proc. New Zealand Inst. 19: 294. 1887 (1886). Type: New Zealand, Waipawa Co., near Norsewood, 1886, *Colenso 1407* (BM!, G!).

Plants small, fragile, easily broken when dry, prostrate, glaucous green to brownish with age, the leaves dull, milky and opaque when moist, subnitid when dry; shoots to 1.8–2 mm wide. Branching sparsely and pseudo-dichotomously furcate, the branches of *Frullania* type, widely spreading; branch half-leaf ± symmetric, ovate, undivided, nonvittate, tapering to a sharp apex (rarely bidentate); first branch underleaf 3-lobed, inserted on ventral-lateral side of juncture of main axis and branch, free from underleaf of main axis. Ventral-intercalary leafy branches often produced, the branching in some populations almost exclusively intercalary; stoloniform branches sporadically present, rarely reverting to leafy branches. Stems slender, the cortical cells firm, with moderately thickened walls, with a fine granular coating like that of the leaves. Leaves alternate, horizontal, contiguous to weakly imbricate, much of stem exposed in dorsal aspect, widely spreading (ca. 90°), plane to weakly convex; leaves vittate, (295)325–490 μm wide × (565)630–925 μm long, strongly incubous, asymmetrically ovate, tapering to a somewhat obliquely truncate apex; apex ± symmetrically tridentate, the teeth ± inflexed, acute to acuminate (rarely blunt), 5–8 cells wide at base, terminating in a uniseriate row of 2–3 cells, the apex otherwise entire; dorsal margin strongly ampliate, distinctly arched, but only weakly auriculate, extending to middle of stem, entire, not decurrent; ventral margin nearly straight, entire, short-decurrent. Vittae of leaves distinct but obscured by the dense granular coating of the leaf, running parallel to and 2–3 cells within the ventral margin at midpoint of leaf, the vitta of 4(6) cell rows; cells of vitta 18–27 μm wide × (20)25–37 μm long, with large, bulging trigones; cells outside the vitta swollen, much smaller, 12–19 μm wide and long, without or with indistinct trigones; surface glaucous and densely and finely punctate-

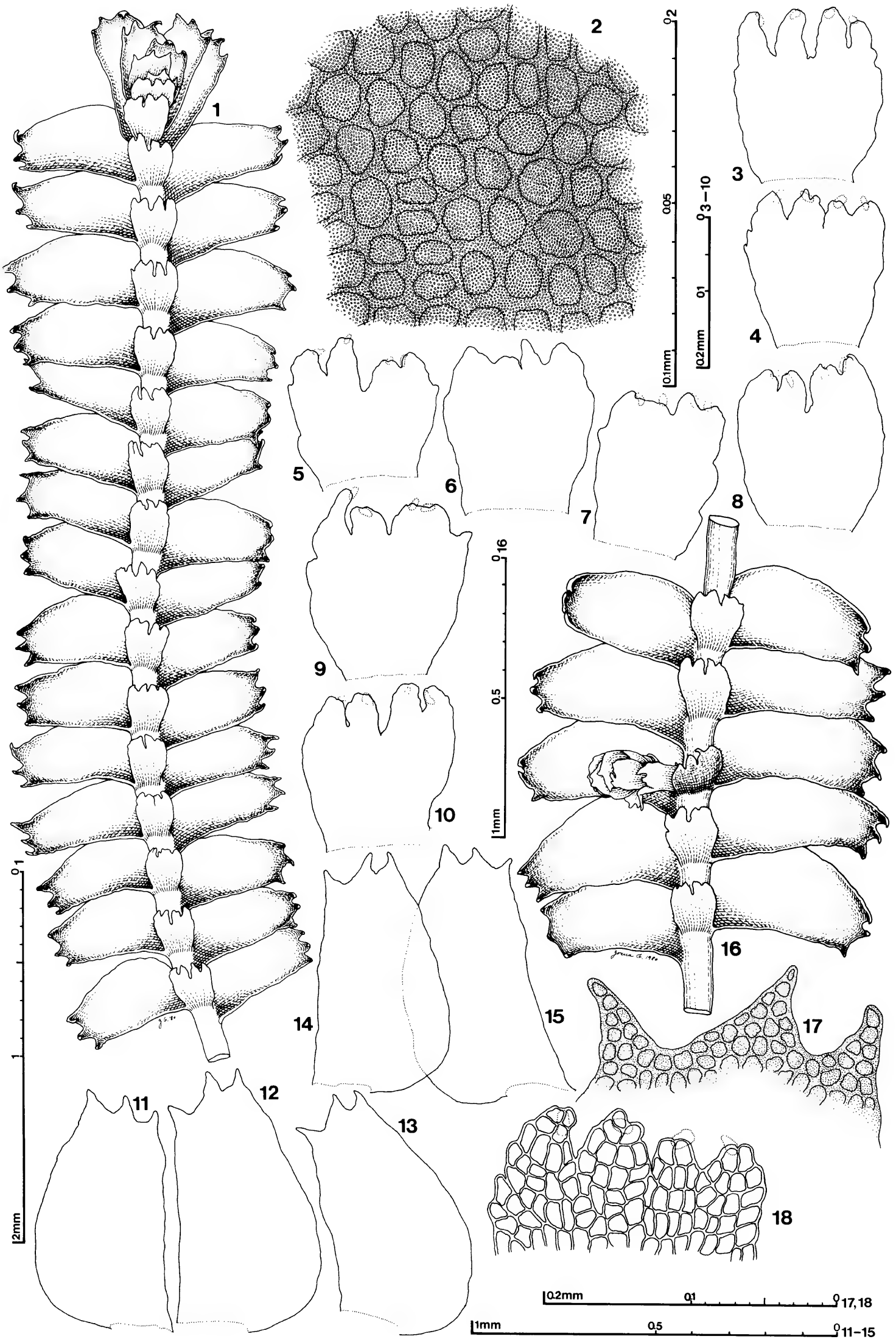

Fig. 103.
Bazzania tayloriana (Mitt.) Kuntze. 1. Axis, ventral view. 2. Median leaf cells in nonvittate portion of leaf; note papillae on surface. 3–10. Underleaves, all from same axis. 11–15. Leaves. 16. Portion

granular. Oil-bodies occupying a conspicuous part of the cell lumen, hazy and opaque, markedly cloud-like, 3–5(6) per vitta cell, 8–9 × 18–19 μm, some 7.5 × 14 μm, irregularly bulging and turgid in appearance, potato- to sausage-shaped, often constricted at the septa, the septa complete but at times appearing incomplete, the oil-bodies homogeneous, many completely aseptate but often others with several segments per oil-body, each oil-body, when segmented, consisting of 2–3(4) large, bulging spheres; oil-bodies in non-vitta cells 2(3) per cell, 5 × 7.5–11 μm; oil-bodies of marginal cells sometimes spherical and 4.5 μm in diam. Underleaves inconspicuous, membranous and colorless throughout, often appearing hyaline, narrowly connate to leaf on one side (rarely free), appressed to the stem, distant, plane, subquadrate, ± equally 4-lobed to ca. 0.2–0.3 or the underleaves bisbifid (the median sinus deeper) or 2(3)-lobed, the lobes ± united in pairs; lobes spatulate, 4–5 cells wide at base, entire to indistinctly serrulate, the apex bluntly rounded, terminating in 2–4 laterally juxtaposed cells (or rarely in a uniseriate row of 2–3 cells), the lobe summit often with a slime papilla; cells of lobes and disc moderately thick-walled, quadrate to ± elongate; disc margins entire; surface finely papillose.

Androecia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from main shoot; bracts ventricose-cucullate, bidentate to short-bilobed, the lobes acute, apiculate; dorsal margin of disc dilated to form a rather well-defined lobule, the lobule margin crenulate and with a few slime papillae, the distal sector with an apical tooth or, when particularly defined, acute and tapering to a sharp summit; antheridia 1 per bract, the stalk biseriate. Gynoecia not seen.

Distribution and Ecology: New Zealand: Stewart Island (100–200 m), South Island (0–ca. 500 m), North Island (100–500[760] m), Chatham Islands (160 m). Known from Fiordland, Westland (Aspiring Natl. Park), Western Nelson, Southern North Island (Tararua Ra.), Volcanic Plateau, Taranaki, Gisborne (Urewera), Auckland (including Great Barrier and Little Barrier islands) and Northland EPs. Common in the North Island, particularly in the upper half of the island; much less common in the South Island. Fulford (1946, 1963b) records the species for Colombia; the Colombia specimens require confirmation. Also reported from Samoa (Miller et al., 1983); this record also requires confirmation.

A species of damp, rich forests (in the North Island *Agathis australis* and *Beilschmiedia tawa – Knightia excelsa* forests; in the South and Stewart islands *Nothofagus*, *Dacrydium cupressinum – Prumnopitys taxifolia* forests and *Metrosideros umbellata – Weinmannia racemosa* forests) where it is found on tree-fern trunks (caudices of *Cyathea dealbata* and *C. smithii*) and caudex bases and old stumps of *Dicksonia squarrosa*, as well as on rotted logs and on humus between and on tree roots at lower to middle elevations (to 500 m on both South and North islands). On Stewart Island (Port Pegasus, vicinity of Tin Ra. Track, ca. 200 m) over a thick layer of soil on a large rocky outcrop in podocarp–hardwood forest including *Dacrydium cupressinum* and *Weinmannia racemosa*. On Chatham Island on a rotten log of *Dracophyllum arboreum*, with *Lepidozia bisbifida* and *Kurzia hippuroides*.

The species is particularly tolerant of deeply shaded niches, such as on humus inside hollow rotting tree stumps or on tree buttresses. In such sites it may be easily identified in the field by the dark bluish green hue. The species often grows shingled or in loosely interwoven pure mats.

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of axis, ventral view, with 1 young ventral-intercalary branch. 17. Leaf apex, with papillae on surface indicated. 18. Underleaf, distal portion. (All from *Child 403*, New Zealand, Kaimai Ra. [F].)

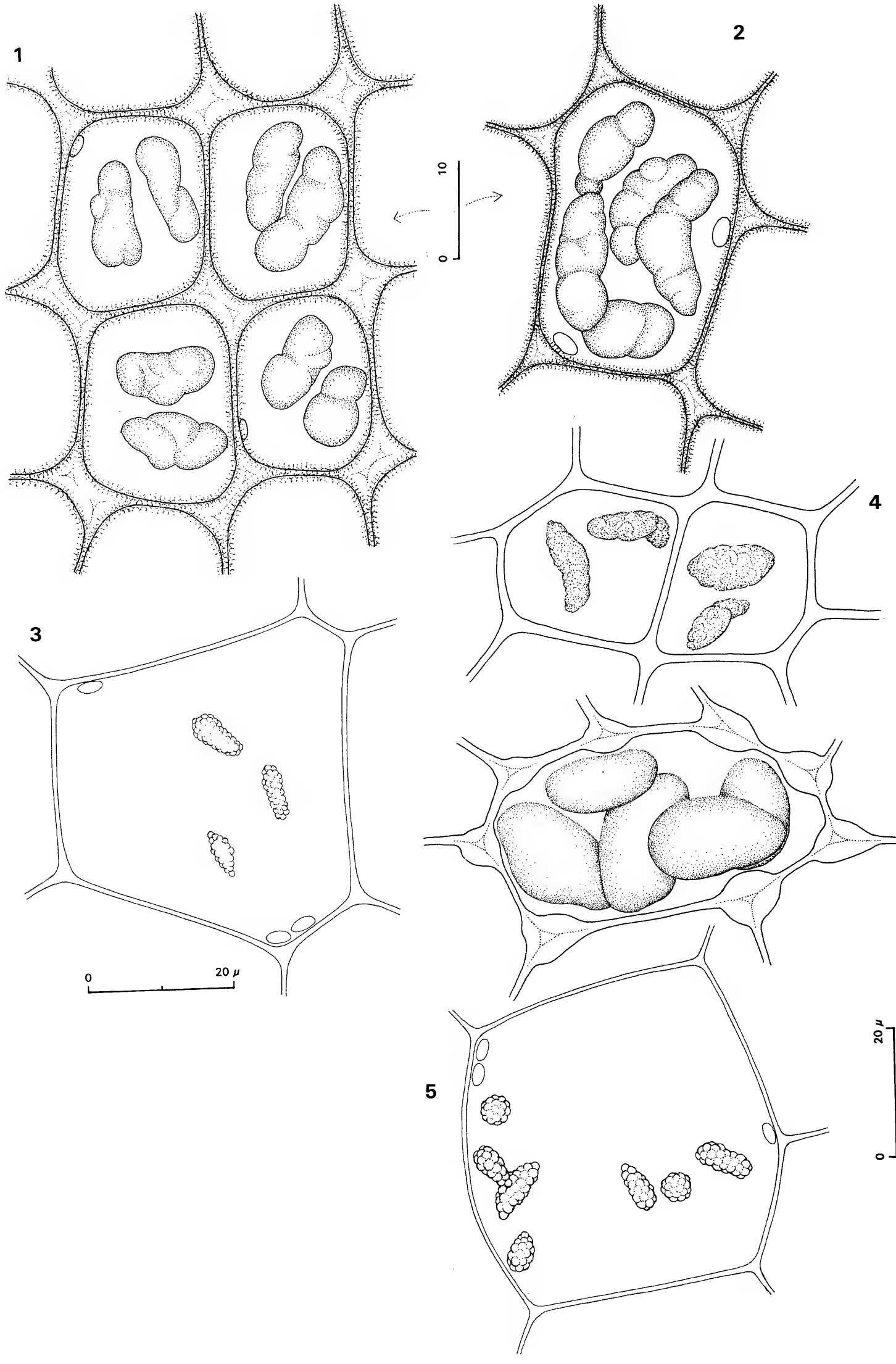

Fig. 104.
Oil-bodies, all (except fig. 4) with the outline of a few chloroplasts included. 1. *Bazzania tayloriana* (Mitt.) Kuntze. Upper middle (non-vitta) cells showing leaf surface detail. 2. *Bazzania taylor-*

Almost invariably accompanied by *Leucobryum candidum*. Other accompanying species are *Bazzania adnexa*, *B. hochstetteri*, *B. nitida*, *Calomnion complanatum* (when on *Cyathea* caudices), *Dicranoloma fasciatum*, *Hymenophyllum revolutum*, *Hymenophyton leptopodum*, *Plagiochila annotina*, *P. lyallii*, *Podomitrium phyllanthus*, *Pyrrhobryum bifarium*, *Rhizogonium distichum*, *R. novae-hollandiae*, *R. pennatum*, *Saccogynidium australe*, *Temnoma pulchellum*, *Trichomanes venosum*, *Zoopsidella caledonica* and *Zoopsis argentea*.

Comments: The leaves are dull and opaque and the leaf cells are obscured by a fine granular coating (Fig. 103: 2), as in *Lepidozia bisbifida* and *Telaranea elegans*. The leaves are often subnitid in dry specimens, but when wetted they appear milky-white and opaque. The underleaves are also characteristic in appearance, with their membranous texture and spatulate lobes (Fig. 103: 3–10). The underleaves are connate on only one side (i.e., the leaves are alternate), and the first branch underleaf is not connate with a stem underleaf.

Sect. ***Exemptae*** J.J.Engel

Bazzania sect. *Exemptae* J.J.Engel, J. Hattori Bot. Lab. 99: 200. 2006. Type: *Bazzania exempta* J.J.Engel.

Bazzania exempta J.J.Engel

[Figs. 105, 106]

Bazzania exempta J.J.Engel, J. Hattori Bot. Lab. 99: 197. *f. 1, 2*. 2006. Holotype: New Zealand, North Is., Wellington Prov., Tongariro Natl. Park, Mangawhero River near juncture of Rimu Track and Forest Walk, just NE of Ohakune, 625 m, *Engel 22709* (F); isotype: (AK).

Plants strongly anisophyllous, delicate and fragile, soft and flexuous, prostrate and growing very loosely on substrate, pale olive-green, the older shoots becoming more deeply so; shoots medium, to 3 mm wide. Branching common, monopodial and not pseudo-dichotomous, the branches nearly exclusively ventral-intercalary, either leafy and then often becoming leading shoots or stoloniform and geotropic, with very reduced scale-like leaves and underleaves; *Frullania*-type branches very rare (one branch seen). Stems ± slender. Rhizoids from stem at immediate bases of both underleaves and leaves of stoloniform branches or from basal cells of the underleaves and leaves; rhizoids sporadically developed on leading leafy shoots, from stem at immediate base of underleaves. Leaves caducous, subopposite, horizontal, spreading at ca. 90° from stem, approximate to barely and loosely imbricate, with much of stem exposed in dorsal aspect; leaves not vittate, 400–550 μm wide × 1200–1500 μm long, distinctly

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iana (Mitt.) Kuntze. Vitta cell from median sector of leaf, showing leaf surface detail. 3. *Pseudocephalozia lepidozioides* R.M.Schust. Disc cell. 4. *Bazzania monilinervis* (Lehm. & Lindenb.) Trevis. Non-vitta cell (upper) (× 1865) and vitta cell (× 1265). 5. *Pseudocephalozia paludicola* R.M.Schust. Disc cell. (Figs. 1, 2, from *Glenny 9130*, New Zealand, South Is., Nelson, Mt. Burnett, saddle between Mt. Burnett and Three Sisters; 3, from *Glenny 9141*, New Zealand, South Is., Westland EP, Mt. Turiwhate; 4, from *Engel 22365*, New Zealand, North Is., Coromandel State Forest Park, Table Mtn.; 5, from *Glenny 9100*, New Zealand, South Is., Westland EP, Mt. Brown.)

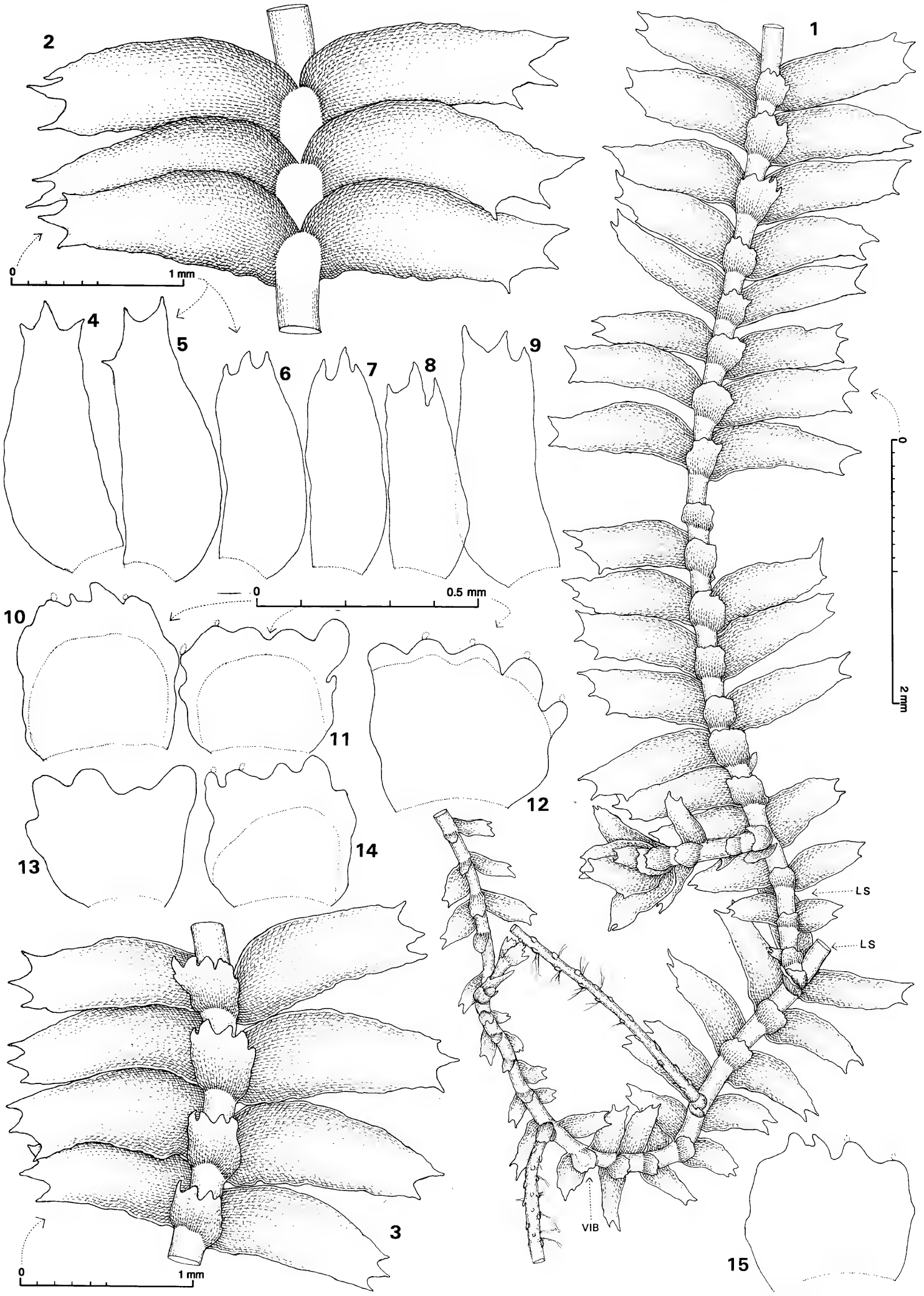

Fig. 105.
Bazzania exempta J.J.Engel. 1. Plant, ventral view, showing caducous leaves and solely ventral-intercalary branching. Note 3 leafy branches, 2 of them leading shoots (= LS), and 2 stoloniform branches; VIB = ventral-intercalary branch within underleaf axil. 2. Portion of plant, dorsal view. 3. Portion of plant, ventral view. 4–9. Leaves. 10–15. Underleaves, the zone of hyaline, decolorate cells is distal to the stippled line (not shown in some); all drawn to same scale. (All from type.)

incubous, plane or the distal sector of the leaf weakly deflexed, the leaves symmetrically to asymmetrically sublinear-ligulate, straight or weakly falcate; apex straight or, often, moderately oblique, asymmetrically (2)3-dentate, the median tooth the largest or the 2 dorsal teeth subequal in size but larger than the ventral tooth, which is often basal in juxtaposition to the median tooth, the ventral tooth at times comprised of only a few cells, the teeth acute to subacuminate, terminating in a single cell or a uniseriate row of 2(3) cells, the terminal cell tapering to a rounded, thick-walled summit, the leaf apex otherwise entire; dorsal margin variable, not ampliate (the leaves then ± symmetric) to moderately ampliate and broadly and gently arched (the leaves then ± asymmetric), usually not extending to middle of stem, subcordate at base, the margin somewhat irregularly repand, otherwise entire; ventral margin straight, often irregularly weakly repand, entire. Cells of leaf differentiated into a broad band of enlarged, subisodiametric to at most slightly elongated cells in the median longitudinal portion of the leaf (a subvitta), the subvitta occupying most of leaf width; cells smaller and subquadrate near the margins; median cells slightly longer than wide, 23–29 μm wide × 24–34 μm long, thin-walled, with trigones lacking or at most straight-sided and inconspicuous, the cells surrounded mostly by the thin cell walls, the trigones somewhat more strongly developed near the margins and at the leaf apex (where they may be medium and straight-sided); surface smooth. Underleaves weakly to moderately spreading, free on both sides, the shape somewhat variable: quadrate to sporadically subcuneate, to suboblate and then broader than long, or subrectangular and then slightly longer than broad; apex ± regularly to somewhat irregularly 4–5-lobulate to ca. 0.1–0.2 and with sinuses often of unequal depth, the lobules rounded at the summit and terminating in a slime papilla, variable in size and at times reduced to a low bulge consisting of several laterally juxtaposed cells with a median-placed slime papilla, the lobe margins entire; apex hyaline (decolorate) distally, the hyaline sector variable in size, often restricted to a zone that includes only the lobes, at times occupying as much as the distal 0.35 of underleaf; margins of disc entire, often repand, occasionally with a tooth or lobule in median sector, often subcordate at the base; cells with walls thin, trigones and surface as in leaves. Asexual reproduction by caducous leaves, the complete leaf falling away, or, often, the leaf base remaining.

Androecia and gynoecia not seen.

Comments: This species differs from all other representatives of the genus by the near absence of terminal branching (only one seen). Branching is monopodial and nearly strictly ventral-intercalary, with both stoloniform and leafy branches present (Fig. 105: 1). The leafy branches are common and become leading shoots that, in turn, produce a ventral-intercalary leafy branch (Fig. 105: 1). Shoots may produce several leafy branches in rather close proximity, but no branching pattern of any sort ensues. Since the plants virtually entirely lack *Frullania*-type branching, the freely and repeatedly pseudo-dichotomous branching pattern that is so typical of the genus is absent.

The species is also unusual in having intramarginal cell walls uniformly thin and with trigones lacking or at most minute (Fig. 106: 1, 2). Trigones are developed only near the margins and at the leaf apex and in both loci they may be medium and straight-sided (Fig. 106: 2, 3). In both cases, however, the cells are surrounded mostly by the thin walls (Fig. 106: 1 right, 2, 3). The genus *Bazzania* typically has cell walls slightly to distinctly thickened, particularly in the subapical sector of the leaf, and trigones that are small to bulging and nodulose.

The leaves are caducous, but somewhat irregularly so—the complete leaf may fall away (Fig. 105: 1), or, frequently, the majority of the leaf may fall away and only the base remains.

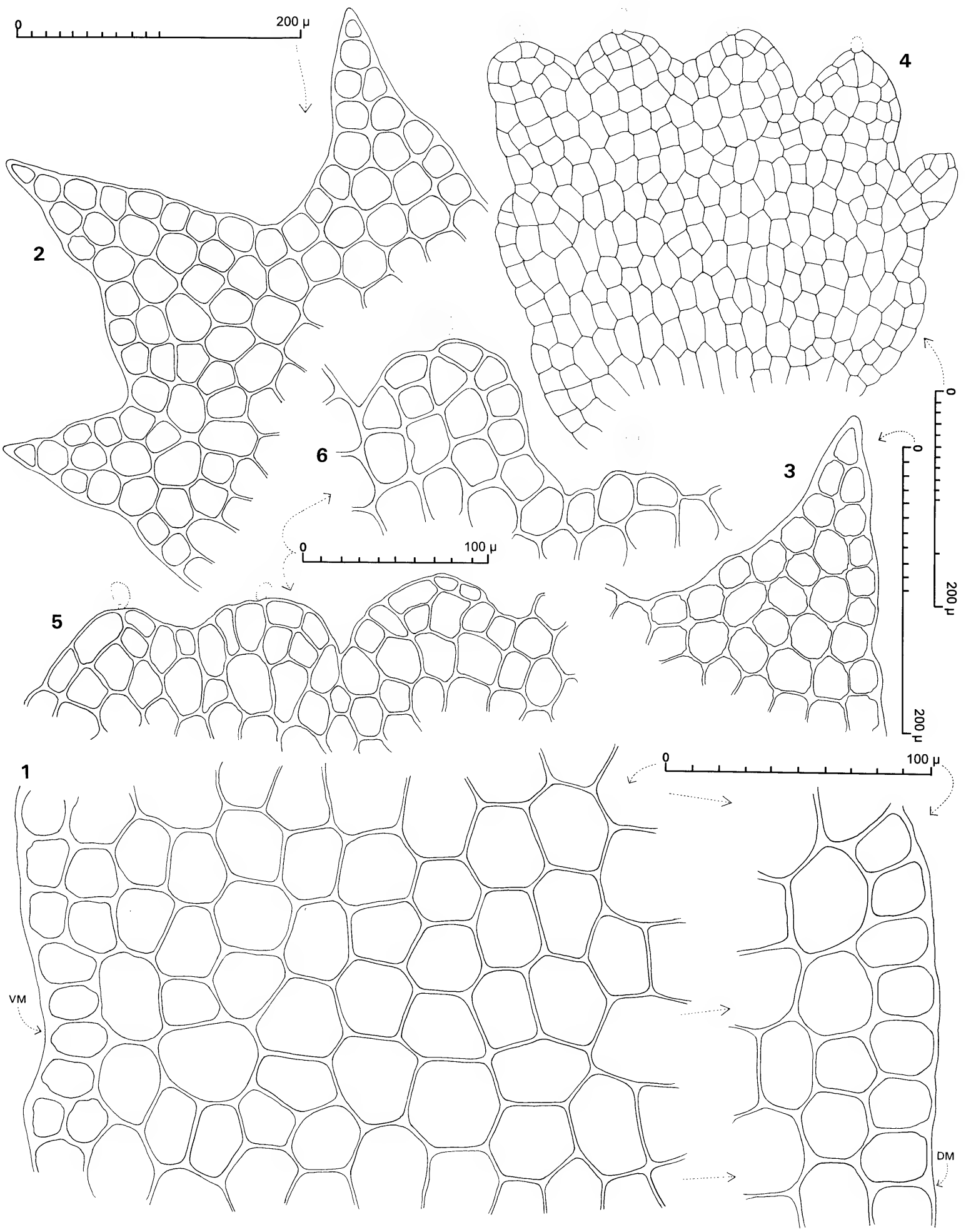

Fig. 106.
Bazzania exempta J.J.Engel. 1. Median sector of leaf, the ventral margin at left (= VM), the dorsal at right (= DM); note the subvitta is comprised of thin-walled cells with at most small trigones. 2. Distal sector of leaf. 3. Dorsal-most lobe of leaf. 4. Underleaf. 5, 6. Underleaf apices. (All from type.)

The arrangement and form of the leaf are distinctive. The leaves are horizontal, spread at about 90° from the stem and are essentially plane, although the distal sector at times is feebly deflexed (Fig. 105: 2). Leaf shape is somewhat variable and grades from symmetrically to asymmetrically sublinear-ligulate, even on the same axis (Fig. 105: 4–9). This variation is largely due to differences in the curvature of the dorsal margin: when the margin is not or only feebly ampliate, the leaves are then ± symmetric and oriented straight (Fig. 105: 7), but when the margin is moderately ampliate and broadly and gently arched, the leaves are then ± asymmetric and weakly falcate (Fig. 105: 4, 5).

Subfam. ***Zoopsidoideae*** R.M.Schust.

Subfamily *Zoopsidoideae* R.M.Schust., Hepat. Anthocerotae N. Amer. 2: 12. 1969.

Pseudocephalozia R.M.Schust.

Pseudocephalozia R.M.Schust., Nova Hedwigia 10: 21. 1965.

Plants often fleshy, soft, pellucid whitish green to pale brown, medium-sized, the leafy shoots to 2.7 mm wide. Plants usually with a system of basal, creeping to geotropic, small-leaved, microphyllous, strongly elongated, often copiously branched stoloniform axes from which arise ascending to erect leafy shoots that are simple or once-branched. Branching nearly exclusively ventral- and lateral-intercalary, rarely of *Frullania* and/or *Microlepidozia* type, the lower parts of leafy branches small-leaved. Stems with a distinct hyaloderm (at times ill-defined on erect leafy axes), the cortical cells thin-walled or with the exterior wall thickened, in up to 12 rows in ours (to 31 in extraterritorial species); medullary cells thin-walled. Rhizoids at bases of leaves and underleaves on stoloniform axes, restricted to underleaf bases on leafy axes, the tips sometimes swollen and "mycorrhizal." Leaves unistratose (in ours) or 2–5-stratose in median to basal sectors (subg. *Lobulatae* (R.M.Schust) R.M.Schust., South America), transversely to clearly succubous in insertion and orientation, the insertion extending to stem midline dorsally; leaves mostly obtrapezoidal, weakly to deeply concave to cucullate, 3–4(6)-dentate to -lobulate to 0.4–0.65 or less; lobes generally sharply acute to acuminate, the margins entire; disc usually 7–8 or more cells high. Cells thin-walled, trigones minute to small or lacking; surface smooth or slightly roughened or striolate. Oil-bodies colorless, large and conspicuous, botryoidal, (1)2–6 per cell. Underleaves variable, some large, (2)3–4-lobed, wider than stem and with a conspicuous disc, others small and scale-like, with 2–4 reduced, 1–few-celled lobes and with a vestigial disc 1–few cells high. Asexual reproduction lacking.

Plants dioecious. Androecia subspicate, becoming intercalary on short or long ventral-intercalary branches or (at times in *Pseudocephalozia cucullata*) intercalary on main shoot; bracts deeply concave to subnavicullariform, the apices 2–3-dentate to -lobate; antheridia 1–2 per bract, the stalk 1- or 2-seriate; bracteolar antheridia occasional, the androecia then isophyllous. Gynoecia on abbreviated to rather short lateral- or ventral-intercalary branches; bracts of innermost series 2–4-stratose toward base or unistratose throughout, the apices 2–4-lobulate

or -lobate, the lamina margins entire or with a few slime papillae and/or a few small teeth, rarely with a lobe; bracteoles similar or identical to bracts. Perianth terete below and feebly to distinctly bluntly trigonous above, at times obscurely 5-plicate distally, or (*P. lobulata*) 4–5-plicate throughout; perianth contracted toward the mouth, the mouth lobulate, the lobe apices either crenulate-denticulate by short (*P. lobulata*) or more often elongate cells that are laterally free for varying distances, or the lobes terminating in a single elongated cell or 2 laterally juxtaposed elongated cells; perianth polystratose toward base, unistratose above. Calyptra extending ca. 0.75 perianth length.

Seta with 8–20 rows of large outer cells and 10–23 rows of small internal cells. Capsule ellipsoidal, the wall 3(sporadically very locally 2)-stratose (in ours) or 3–4-stratose; outer layer of cells with two-phase development, the longitudinal walls with continuous sheets of secondary wall material, often extended as nodules, alternating with primary walls devoid of thickenings; inner cells with a few and weak, often incomplete, semiannular bands.

Spores vermiculate, at times irregularly areolate. Elaters rather rigid, at most feebly tortuous, bispiral.

Type: *Pseudocephalozia paludicola* R.M.Schust.

A genus of six species. Three are Australasian (subg. *Pseudocephalozia*), of which two occur in New Zealand, and one (*Pseudocephalozia leptodictyon* R.M.Schust.) is known from alpine New Guinea. The other three species (subg. *Lobulatae*) occur in southern South America: one (*P. quadriloba* (Steph.) R.M.Schust.) has an Andean distribution (see Engel, 1978) and extends north at higher elevations (3200–3600 m) in the Andes to Venezuela and disjunct in Costa Rica (at Volván Poás, 2600 m); also on Inaccessible Island; a second species is known from a few collections in the southern sector of the Magellanian zone (*P. cucullata* J.J.Engel & R.M.Schust.) and a third is known only from the type in the Valdivian zone (*P. lobulata* (Herzog) R.M.Schust.).

The two subgenera are sharply divided: subg. *Pseudocephalozia* (our area) has unistratose leaves, underleaves and gynoecial bracts; uniseriate antheridial stalks; and a bistratose capsule wall. Members of subg. *Lobulatae* have multistratose leaves, underleaves and gynoecial bracts; biseriate antheridial stalks; and a 3–4-stratose capsule wall.

References: Schuster and Engel (1974; mon.); Schuster (2000a).

Key to Species

1a. Leaf lobes acute, often apiculate, ending in a uniseriate row of 2–3, hardly elongated cells; leaves (3)4–5(6)-lobed to 0.45; underleaves highly variable, the larger ones with disc 4–6 cells high; leafy branches indiscriminately lateral- and ventral-intercalary, with sporadic *Frullania*-type branches present; bracteolar antheridia present . . . . . *P. paludicola* (p. 459)

1b. Leaf lobes long-acute to acuminate, ending in a uniseriate row of 3–6, usually elongated cells; leaves 3–4(5)-lobed to 0.65; underleaves uniformly small and reduced, the disc 1–2 cells high; leafy branches mostly lateral-intercalary, usually no *Frullania*-type branches present; bracteolar antheridia absent . . . . . *P. lepidozioides* (p. 461)

Pseudocephalozia paludicola R.M.Schust.

[Fig. 104: 5, oil-bodies, p. 452; Fig. 107]

Pseudocephalozia paludicola R.M.Schust., Nova Hedwigia 10: 21. 1965. Holotype: Tasmania, Lake St. Clair Natl. Park, E slope of Mt. Rufus, ca. 3800–4100 ft., *Schuster 50512* (F!).

Plants with leafy shoots erect to suberect, vivid green distally, whitish green below, to 1.1 mm wide. Branching copious, intercalary, indiscriminately from axils of leaves and underleaves, rarely with isolated *Frullania*-type branches present; stoloniform axes abundant, microphyllous, very remote-leaved, but often distally becoming leafy and erect, the main leafy shoots occasionally becoming stoloniform. Stems with a hyaloderm of large, thin-walled cortical cells in 10–12 rows and a small-celled medulla 4–8 cells across. Rhizoids abundant on microphyllous axes, arising from bases of leaves and underleaves, with swollen, mycorrhiza-like tips. Leaves unistratose, contiguous to weakly imbricate above, extremely variable, obtrapezoidal to sporadically reniform-obtrapezoidal, strongly concave, the lobes usually erect or even incurved, the insertion weakly succubous, 620–1100 μm wide × 500–700 μm long, the apex (3)4–5(6)-lobed to 0.35–0.45; lobes acute, commonly apiculate, 3–6 cells wide at base, terminating in a short uniseriate row of 2–3, scarcely elongated cells; disc usually 6–10 cells high, 15–22 cells wide in 3–4-lobed leaves (to 25–29 cells wide in 5–6-lobed leaves). Cells delicate and thin-walled, variable, polygonal, the median cells 28–42 μm wide × 36–62 μm long; surface smooth. Oil-bodies occupying a very small part of cell, small for cell size, hyaline and glistening, 4–8 per disc cell, coarsely papillose, quickly breaking up, coalescing and appearing very coarsely botryoidal, the oil-bodies globose, 4–5 μm in diam. Underleaves highly polymorphic, even on one stem, the larger underleaves (2)3–4-lobed, 0.75 the size of the leaves, the disc 4–6 cells high, the lobes resembling those of the leaves; smaller underleaves 2–3-lobed, with disc only 1–2 cells high, the lobes consisting of 1–2 elongated cells, terminating in a slime papilla.

Androecia compactly spicate, small, on abbreviated lateral- and sometimes ventral-intercalary branches; bracts in 2–4 cycles, small, imbricate, pouched, 3-lobed; antheridia 1 per bract, the stalk uniseriate; bracteolar antheridia sometimes present, 1–2-androus. Gynoecia on very abbreviated branches originating from stoloniform axes; bracts of innermost series with apices 4-lobulate, the 2 median lobes larger, the 2 stronger lobules terminating in a single cell or a uniseriate row of 2–3 cells; the lamina margins with a few 1–few-celled teeth each terminating in a slime papilla or crenulate by projecting upper ends of cells; bracteoles identical to bracts or somewhat smaller. Perianth terete below and bluntly trigonous in distal ca. 0.25, contracted toward the mouth, the mouth lobulate, the lobules each with the summit crenulate by cells laterally free for varying distances, the terminal cells somewhat elongated, rounded at the summit and not sharp; perianth 2–3-stratose toward base, unistratose above.

Seta with 8–9 rows of large outer cells surrounding ca. 23 rows of small internal cells. Capsule ellipsoidal, the wall 3(sporadically very locally 2)-stratose, 30–31 μm thick; outer layer of cells with two-phase development, the primary walls lacking pigmented thickenings, the secondary walls longitudinal but sporadically also transverse, the longitudinal walls (and the transverse, when present) with thin continuous sheets of pigmented wall material and with nodular thickenings only feebly developed, lending the walls a sinuous appearance; inner layer of cells elongate-rectangular, with semiannular bands common, narrow and pale, the bands at times incomplete, the thickenings then nodular to spine-like.

Spores 12.5–13.4 μm in diam., pale yellow-brown, with low but sharply defined vermiculate markings that often fork and anastomose to delimit irregular areolae. Elaters rigid, at most feebly tortuous, 10.6–11.5 μm wide, bispiral to tips, the spirals 4.3–4.8 μm wide.

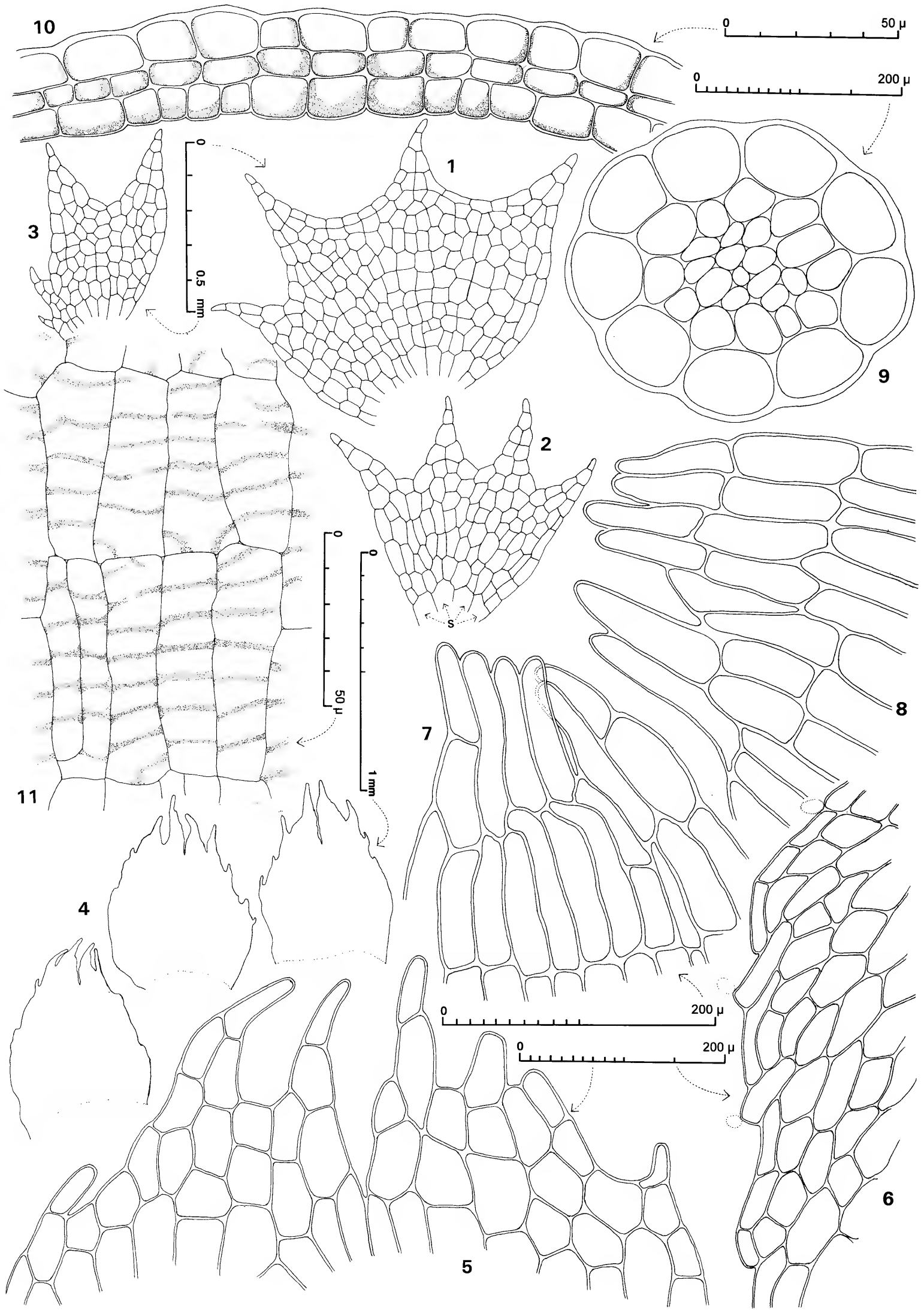

Fig. 107.
Pseudocephalozia paludicola R.M.Schust. 1, 2. Large and smaller leaves (S = stem cells at base of lower leaf); drawn to same scale. 3. Bilobed underleaf. 4. ♀ Bracts and in middle, bracteole. 5.

Distribution and Ecology: New Zealand: Antipodes Islands (140 m), Stewart Island (20–30 m), South Island (390–1600 m), North Island (950 m); Australia: Tasmania, Victoria. In New Zealand known from Otago, Westland, Canterbury, Nelson and Volcanic Plateau EPs.

Known from a few scattered, rather open sites in New Zealand. The species is usually found on boggy or swampy peaty soils, but the habitat varies between small clearings in open low forest or tall scrub, sparse tussockland or rushland in seepages and open cushionfield dominated by *Sphagnum cristatum* and *S. falcatulum*. On Stewart Island on a clayey bank at 20–30 m along a stream in a regenerating forest dominated by *Fuchsia excorticata* and *Griselinia littoralis* canopy and *Blechnum discolor* understory (Fern Gully Track). In the South Island on the summit plateau of Mt. Maungatua (30 km W of Dunedin, 825 m), occurring in tussock grassland with a mosaic of scattered bogs having abundant *Sphagnum* and patches of *Dracophyllum*, *Halocarpus bidwillii*, *Hebe* and *Donatia*. At this site the species occurred over peaty soil in moist sites (e.g., in a protected niche under *Halocarpus bidwillii*) or in very wet sites, such as on saturated soil or in small pools. Also in the Paparoa Ra. (Croesus Track, 420 m), occurring on the floor of a steep slope under scrubby vegetation in an area of landslip covered with low scrub vegetation along with abundant bryophytes, *Lycopodium* and *Blechnum*. In the North Island on Mt. Ruapehu (near Ohakune Mtn. Road, ca. 950 m) in a swampy area with *Libocedrus*, *Nothofagus* and *Metrosideros*. Other bryophytes found in association with *Pseudocephalozia paludicola* have been *Balantiopsis verrucosa*, *Campylopus clavatus*, *Dicranophyllum crispulum*, *D. pulchellum*, *Kurzia helophila* and *Pachyschistochila berggrenii*.

Comments: A highly malleable species, the underleaves range, often on the same stem, from few-celled and minute (as in *Pseudocephalozia lepidozioides*) to large, with a large disc and lobes like those of the leaves. The production of large, rather leaf-like underleaves, with a disc 4–6 cells high and 8–10 cells broad, will at once distinguish the species from *P. lepidozioides*, which has uniformly small, vestigial underleaves. The leaves range from 3- to 6-lobed and from obtrapezoidal to broad and almost reniform. Branching is perhaps 95% intercalary, but terminal, *Frullania*-type branches are also sporadically produced. The abbreviated branches are, at least normally, intercalary in the axils of lateral leaves, but at least the androecia may be ventral-intercalary. Lateral-intercalary androecia have reduced bracteoles that are few-celled, flat and lack antheridia, but ventral-intercalary androecia are tristichous, the bracteoles inflated, with 1–2 associated antheridia.

Pseudocephalozia lepidozioides R.M.Schust.

[Plate 8D; Fig. 104: 3, oil-bodies, p. 452]

Pseudocephalozia lepidozioides R.M.Schust., Nova Hedwigia 10: 22. 1965. Holotype: New Zealand, South Is., Fiordland, Doubtful Sound Track, W of Lake Manapouri, between Wilmot Pass and Spey River, along Dashwood Stream, 450–480 m, *Schuster 52610b* (F!).

Lepidozia leptodictyon Herzog, Trans. & Proc. Roy. Soc. New Zealand 68: 45. 1938. *Micrisophylla leptodictyon* (Herzog) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 71. 1965, *non*

Distal sector of ♀ bract. 6. Portion of lateral margin of innermost ♀ bract. 7, 8. Portions of perianth mouth (drawn to same scale). 9. Seta, cross section. 10. Capsule wall, cross section. 11. Capsule wall, inner layer. (All from *Engel 17738*, New Zealand, South Is., Otago EP, summit plateau of Mt. Maungatua.)

Pseudocephalozia leptodictyon R.M.Schust., J. Hattori Bot. Lab. 36: 349. *f.* 6. 1973 (1972) (New Guinea). Holotype: New Zealand, North Is., near Atiamuri, ca. 1000 ft., 18 July 1929, *Allison 70* (JE!); isotype: (MPN!).

Plants bright, pellucid green, nitid when dry, to 1.7 mm wide. Branching intercalary, always (or nearly always) from ventral part of axils of lateral leaves, with *Frullania*-type branches rare or sporadic (and present in some populations only); stoloniform ventral-intercalary branches sparingly produced at base; leafy shoots occasionally flagelliform and geotropic at apices. Stems with a soft-textured cortex of 8–12 rows of large, thin-walled cells, the medulla of much smaller, delicate, leptodermous cells, 5–6 cells across. Rhizoids frequently produced from bases of underleaves on leafy shoots, on stoloniform axes from leaf- and underleaf-bases. Leaves unistratose, rather strongly and stiffly spreading, obtrapezoidal, 4(5)-lobed to 0.5, sporadically 3-lobed on weak stems, 5-lobed on unusually vigorous ones, 3–4-lobed to 0.65 in some populations, the sinuses V- to broadly U-shaped, the leaves somewhat succubously inserted but subtransversely oriented, 775–850 μm wide at apices, 600–685 μm long; lobes divergent, straight, rarely clearly incurved, narrowly acute to short-acuminate and 4–8 cells broad at base, to long-acuminate and (2)3–4 cells broad at base, terminating in a uniseriate row of (2)3–4(7) slightly to strongly elongated cells that are progressively smaller distally; disc 3–5 to 6–8 cells high, clearly narrowed to base, with margins almost straight or weakly arched. Cells leptodermous, delicate, polygonal, the median cells 36–48 μm wide × (42)50–75(80) μm long, the basal cells 45–65 μm wide × 65–90 μm long; surface smooth. Oil-bodies occupying a small portion of cell, hyaline, 2–4 per median disc cell, botryoidal, the globules distinctly protruding beyond the membrane, the oil-bodies elliptic to often ± fusiform, 3.5–4.5 × 8–11 μm, occasionally spherical and then 3.5–5 μm in diam.; basal cells with no oil-bodies or 2, lobes with same number per cell as midleaf. Underleaves small to very small, at most 165–200(220) μm wide and long but usually much smaller, only 4–6 cells wide, inserted on 2–3(4) stem cortical cells; lobes rudimentary and finger-like, consisting of 1–2(3) elongated cells (often 1–2 lobes aborted and only 1-celled), terminating in a slime papilla; disc of 1–2 tiers of small, subisodiametric cells. Fungal partner an ascomycete?

Androecia not seen. Gynoecia on abbreviated, lateral-intercalary branches, the perianths seeming nearly sessile on main stems; bracts in 2 series, small, those of inner series subovate, erect-appressed, irregularly lobulate distally; bracteoles similar. Perianth firm, cylindrical and hardly trigonous distally, contracted to mouth, the mouth lobulate, the lobe apices crenulate-setulose with pointed, narrow, tapered cells, 13–16 × (60)80–120(148) μm, free only at their tips; perianth bistratose basally.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (5–530 m), South Island (700–1480 m), North Island (60–1320 m). Known from Fiordland, Westland, Canterbury (at the Main Divide), Western Nelson, Volcanic Plateau, Gisborne and Northland (Waipoua, Radar Bush) EPs.

With a scattered but widespread distribution over much of New Zealand. Found on soil and decomposing leaf litter in a variety of habitats ranging from forest and scrub to flushes in tussockland and on the margins and floors of small tarns. On Stewart Island at the summit area of Mt. Rocky (530 m) it occurs creeping among *Leucobryum* on ground under stunted *Leptospermum scoparium*, *Olearia* and *Gahnia* in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus*. Also at

5 m on Stewart Island (track to Mason Bay, ca. 1–1.8 km W of Freshwater Landing) on an old dead *Leptospermum scoparium* base in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. The type (near Wilmot Pass, Fiordland) occurred over wet, somewhat peaty soil among rocks, on a *Nothofagus menziesii* forest–dominated slope, associated with *Lembidium nutans*, *Megalembidium insulanum*, *Haplomitrium gibbsiae*, *Treubia lacunosa*, *Heteroscyphus* sp. and several *Lepidozia* and *Riccardia* spp. At the summit area of Arthur's Pass (920 m) it was found on the floor among shrubs in a mosaic of penalpine scrub and alpine vegetation. On the ridge above Te Kuha (E of Westport, 700 m) it occurs under *Lepidothamnus intermedius* scrub 3 m tall, with *Chiloscyphus spiniferus*, *Leptoscyphus australis*, *Plagiochila ramosissima* and *Riccardia perspicua*. Also at higher elevations, in Nelson Lakes Natl. Park (vicinity of Mt. Robert Skifield, 1400–1480 m) in an area of tarns in low alpine vegetation. At this site the species occurs under prostrate mats of dead tussock blades (a niche that at midday appeared to be warmer than surrounding niches in the vicinity) as well as with *Sphagnum* at the edge of a tarn. Also under prostrate layers of tussock blades at the summit area of Te Rangaakapua (Huiarau Ra., Urewera Natl. Park, 1265–1320 m) in a mosaic of stunted *Olearia colensoi* and tussock with occasional *Coprosma* spp. Also occurring in a *Leptospermum scoparium – Dracophyllum subulatum* scrub ecotone at Tree Trunk Gorge (E border of Tongariro Natl. Park, 750 m). The species ranges to the far north of North Island at Radar Bush (WSW of Cape Reinga); at this site the species occurs on soil at the base of *Cyathea* at the bottom of a steep-sided valley within a forest of *Beilschmiedia – Vitex – Hoheria* and *Cyathea dealbata*.

Comments: Closely allied to *Pseudocephalozia paludicola* in the leaves divided to about 0.5, the rather long, uniseriate antheridial stalks and the vigorous shoots with some 5-lobed leaves. It differs from this species in the more attenuate leaf lobes and generally larger cell size, in the consistently vestigial underleaves and the lack of bracteolar antheridia. The bright green color is distinctive in the field.

Paracromastigum Fulford & J.Taylor

Paracromastigum Fulford & J.Taylor, Brittonia 13: 336. 1961.
Bonneria Fulford & J.Taylor, Brittonia 13: 334. 1961.
Leucosarmentum Fulford, Mem. New York Bot. Gard. 11: 386. 1968.

Plants anisophyllous, procumbent, pale green to brownish, typically with an extensive system of stoloniform axes with reduced, bidentate or bilobed leaves; plants small, mostly to 375 μm wide. Branching irregular, the branches variable, predominantly ventral-intercalary, at times also lateral-intercalary; *Acromastigum*-type branches (only rarely lacking) and *Frullania*-type branches common, sometimes with *Microlepidozia*-type branches (with all 3 types of terminal branches present in some species). Stems with cortex mostly firm-walled, occasionally thin-walled, in mostly 7–12 rows (rarely to 17 rows), subequal or weakly to markedly larger than the thin-walled medullary cells. Rhizoids from stem at base of underleaves or from lower cells of underleaf. Leaves remote to feebly imbricate, the insertion (and orientation) variable: weakly incubous and extending to stem midline dorsally (subg. *Paracromastigum*), to weakly to distinctly succubous and with insertion not extending dorsally to stem midline and delimiting a leaf-free strip of 2 cell rows wide (subg. *Austrocephalozia*); leaves concave, 2–3-lobed to 0.35–0.8. Cells thin- to feebly and equally thick-walled, trigones absent, the surface smooth

(when cells leptodermous) or striate-papillose (when cells firm). Oil-bodies lacking or present as small droplets or, in some species, present in some cells, finely to coarsely botryoidal and 1–3 per cell, in *Paracromastigum pachyrhizum* (= *P. bifidum*) 1–2(3) per cell and homogeneous to 3–5-segmented. Underleaves at most 0.6× area of leaves, with 2–4 lobes, the lobes often unequal; disc distinct and several cells high. No asexual reproduction.

Dioecious. Androecia on short, usually ventral- but at times lateral-intercalary branches, often brownish, even if sterile shoots lack pigmentation, spicate; bracts usually in 4–12 to as many as 18 pairs, deeply concave to ventricose, the apices bilobed; antheridia 1 per bract, the stalk 2-seriate; bracteolar antheridia absent or present. Gynoecia on short ventral- and lateral-intercalary branches; bracts of innermost series much larger than leaves, bifid to 0.2–0.6; lobes mostly terminating in a single cell or a uniseriate row of 2–5 cells, the lobe margins with a few teeth or entire; disc margins with small teeth or sparingly crenulate by projecting upper ends of cells; bracteole similar to bracts or a little smaller. Perianth trigonous above, the mouth dentate-ciliolate to lobulate, the teeth usually discrete from one another and terminating in a single cell or a uniseriate row of 2–3 somewhat elongated, at times thick-walled cells, the terminal cell rounded at the summit and not sharp, or (*Paracromastigum longiscyphum*) the mouth comprised of elongate cells that are laterally free for varying distances; perianth unistratose throughout or locally bistratose toward base.

Seta with 8–9 rows of large outer cells and 11–15 rows of much smaller internal cells. Capsule ellipsoidal, the wall 2–3- or 3-stratose; outer layer of cells with two-phase development, the longitudinal walls with obscure to distinct continuous sheets of secondary wall material and nodular (to rarely weakly extending) thickenings, alternating with primary walls with thickenings absent or in a few species weakly developed; inner cells with a few to several semiannular bands and (commonly) nodular thickenings.

Spores and elaters not seen.

Type: *Paracromastigum subsimplex* (Steph.) Fulford & J.Taylor (≡ *Lepidozia subsimplex* Steph.)

A genus of 12 species. Three species occur in southern South America, *Paracromastigum stipulatum* (Herzog) Fulford, *P. subsimplex* (Steph.) Fulford & J.Taylor and *P. dusenii* (Steph.) R.M.Schust., the latter known from the type (Chile, Prov. Aisén) and recently reported from Serra do Itatiaia in eastern Brazil (Gradstein and Pinheiro da Costa, 2003, p. 209). One species occurs in western Australia, *P. longiscyphum* (Taylor) R.M.Schust. & J.J.Engel, one in Tristan da Cunha, *P. tristanianum* (R.M.Schust.) J.J.Engel & R.M.Schust. (the presence of this species in South Africa requires further investigation; see Schuster, 2000a, p. 370), one in South Africa, *P. succulentum* (Sim) J.J.Engel & Merrill (Engel and Merrill, 2001), and four in our area. The remaining species are Neotropical.

References: Schuster and Engel (1996); Schuster (2000a).

The following key is adapted, with considerable modification, from Schuster (2000a).

Key to Species

1a. Leaves clearly succubously inserted and oriented, the lines of insertion not extending to stem midline dorsally, leaving a leaf-free strip of stem cells; main shoots with usually 2–3 cortical cells intervening between successive leaves on either side; plants strongly

anisophyllous, the underleaves few-celled, less than 0.25 the area of leaves; shoots without a conspicuous and extensive system of microphyllous axes and/or stolons; *Frullania*-type branches present. Subg. *Austrocephalozia* 2

2a. Leaves remote to contiguous, strongly laterally spreading; leaf lobes lanceolate, ending in a uniseriate row of 2–3 elongated cells; underleaf disc 1–1.5 cells high; plants pale green . . . . . *P. furcifolium* (p. 468)

2b. Leaves imbricate, somewhat dorsally assurgent; leaf lobes acute, ending in a single cell or a uniseriate row of 2 subisodiametric cells; underleaf disc 3 cells high; plants (sun forms) strongly reddish brown pigmented . . . . . *P. macrostipum* (p. 471)

1b. Leaves with transversely to clearly (if weakly) incubously inserted and oriented, the lines of insertion extending to stem midline dorsally; main shoots with 5–8 cortical cells intervening between successive leaves on either side; plants subisophyllous, the underleaves 0.5–0.65 the area of lateral leaves; leafy axes arising from an extensive system of elongated, microphyllous, stoloniform stems; *Frullania*-type branches mostly lacking. Subg. *Paracromastigum* 3

3a. Leaves and underleaves (2)3–4-lobed; stem with 8–12 cortical cell rows 4

4a. Leaf lobes with cells larger than those of the disc, the few- and large-celled dorsal lobe 3–4 cells wide at base; leaves of mature shoots 7–8(12) cells wide in median sector; oil-bodies present at least in isolated cells, 1 or 2 per cell. Volcanic region of the North Is., on fine-grained, exposed volcanic soils . . . . . *P. drucei* (p. 465)

4b. Leaf lobes with cells similar in size to those of the disc, the dorsal lobe up to 5–9 cells wide at base; leaves of mature shoots 10–21 cells wide in median sector; oil-bodies lacking. Snow tussock (*Chionochloa*) zone of South Is., on peaty ground . . . . . *P. fiordlandiae* (p. 466)

3b. Leaves and underleaves consistently bilobed (isolated exceptions aside); stem with 6 rows of inflated cortical cells . . . . . [see *Hyalolepidozia*, p. 472]

Paracromastigum drucei (R.M.Schust.) R.M.Schust.

Pseudocephalozia drucei R.M.Schust., Nova Hedwigia 10: 22. 1965. *Paracromastigum drucei* (R.M.Schust.) R.M.Schust. *in* R.M.Schust. & J.J.Engel, J. Hattori Bot. Lab. 38: 700. 1974. Holotype: New Zealand, North Is., Mt. Egmont, *Schuster 48979*.

Plants whitish green, becoming tinged with brownish to reddish brown to reddish (at least in exposed sun forms), the shoots minute. Branching copious and irregular, the branches of lateral- and ventral-intercalary types; *Acromastigum*- and *Frullania*-type branches very rarely present; stoloniform axes common. Stems with cortical cells large and thin-walled, in 12 or fewer rows, moderately to distinctly larger than medullary cells, in surface view subquadrate to short-oblong, under 2× as long as wide usually; medullary cells thin-walled. Main shoots with 5–8 cortical cells intervening between successive leaves on either side. Leaves small, very remote, suberect to erect, concave, the concavity turned toward the stem, the insertion transverse to feebly incubous, extending to stem midline dorsally; leaves formed from relatively few cells, 6–8 to 11–12 cells wide in median sector, 6–8 cells wide at the base, 2–3(4)-lobed, the lobes triangular to somewhat attenuate, usually comprised of a few, usually 3–6, large cells, the cells larger than those of the disc, the dorsal lobes 3–4 cells broad at base, the leaves often asymmetrically lobed, the two ventral lobes reduced and only 1–2-celled, each

terminating in a slime papilla, or the lobe reduced to a slime papilla; disc 2–4 cells high. Cells of leaves little or scarcely elongated, thin-walled, devoid of trigones; surface of lobes and disc papillose, the disc at times obscurely so. Oil-bodies (*fide* Schuster, 2000a) present at least in isolated cells, 1 or 2 per cell, colorless, botryoidal. Underleaves ca. 0.5 (rarely more than half) the leaves in size, few-celled, usually asymmetric and with one well-developed lobe formed from 5–6 cells and 2–3 reduced lobes each formed of 1–2 cells, the terminal cells typically reduced to a slime papilla, the half or more of the underleaf that forms reduced lobes distally often develops 2–3 rhizoids from a few small basal cells.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: North Island (1200–1630 m). Known only from the volcanic region of the North Island (Volcanic Plateau and Taranaki EPs), where it occurs as a pioneer on fine-grained, exposed volcanic soils in alpine and penalpine regions.

At the headwaters of Mangawhero River (Tongariro Natl. Park, 1630 m) plants occurred over soil deep in rock crevices in an alpine fellfield. Also at Mangatepopo Stream below Soda Springs (Tongariro Natl. Park, ca. 1200 m) over soil in an area of alpine vegetation with scattered frequent rocky outcrops.

Comments: *Paracromastigum drucei* differs from *P. fiordlandiae* in 1) leaves formed from relatively few cells, 6–8 cells broad at the base and 7–8(12) cells wide in median sector, with lobes of few, usually 3–6, large cells; and 2) underleaves few-celled, typically with one well-developed lobe formed from 5–6 cells and 2–3 reduced lobes each formed of 1–2 cells, the terminal cells typically reduced to a slime papilla. The half or more of the underleaf that forms reduced lobes distally often develops 2–3 rhizoids from a few small basal cells, while the half of the underleaf with the well-developed lobe lacks them. The asymmetry seen in the underleaves at times also occurs in the lateral leaves, with the two ventral lobes reduced and each terminating in a slime papilla. Also, oil-bodies are present, though in isolated cells, vs. completely lacking in *P. fiordlandiae*. Moreover, the ecology of these species is entirely different: *P. drucei* is a pioneer on fine-grained, exposed volcanic soils in alpine and penalpine regions in the volcanic region of the North Island whereas *P. fiordlandiae* is found on peaty ground in the snow tussock (*Chionochloa*) zone of the South Island.

Paracromastigum fiordlandiae R.M.Schust. & J.J.Engel

Paracromastigum fiordlandiae R.M.Schust. & J.J.Engel, Brittonia 48: 167. *f. 1*. 1996. Holotype: New Zealand, South Is., Fiordland Natl. Park, Mt. Burns, Hunter Mtns., 4500–5000 ft., 9 Jan. 1984, *Schuster 84-136* (herb. Schuster).

Plants subisophyllous, soft-textured, fleshy, consisting of interwoven, pale, whitish green, distally brownish or purplish brown pigmented (androecia often more deeply pigmented); shoots thread-like, indefinite in length, ca. 235–285 μm wide with leaves (shoot apices rarely to 325–360 μm wide). Branching copious, nearly exclusively intercalary (85% lateral; 15% ventral); terminal branching very rare (one *Acromastigum*-type branch seen). Stems fleshy, the cortex in sporadically 8 but mostly 9, occasionally ranging to 12, rows, feebly thick-walled, slightly inflated but much larger than the medullary cells and forming a hyaloderm, in surface view subquadrate to short-rectangular, usually under 2× as long as wide; medullary cells in (11)15–24 rows, the peripheral row somewhat thick-walled but toward the center rather thin-walled. Rhizoids rather rare, mostly at bases of highly reduced underleaves low on the stem,

usually 1 or 2 per underleaf base, sporadically from basal cells of underleaves of normal leafy shoots. Main shoots with 6–8 cortical cells intervening between successive leaves on either side. Leaves exceedingly remote, small, their width usually not or barely exceeding stem width but some shoots toward apices with leaves appreciably longer, remaining remote, the insertion (as seen in dorsal aspect) feebly incubous to transverse, extended to stem midline (to the median-longitudinal cell walls), ventrally somewhat obliquely incubous. Mature leaves concave, suberect, hand-like, the lobes erect or more often a little incurved, the leaves when flattened somewhat asymmetrically quadrate-ovate to quadrate-obovate, 400 μm wide × 450 μm long (in the dorsal half, the ventral sector ca. 340 μm long) to 370 μm wide × 540 μm long (then ventrally 500–510 μm long), usually asymmetrically bifid or (less often) trifid for 0.35–0.45 their length; lobes acute (but not long-acute), unequal, the dorsal lobe larger, up to 5–9 cells wide at base, usually terminating in a uniseriate row of 2 cells; ventral 1 or 2 lobes usually a little shorter, few-celled, 4–5 cells broad, blunt at the tips or ending in a single cell and terminating in a slime papilla; leaves exceptionally symmetrically trifid and without reduction of ventral lobe(s); disc 10–21 cells broad, the dorsal margin gently curved, the ventral equally or less so. Cells similar in size throughout leaf, with walls thin in lower half of leaves, a little thickened in the (often pigmented) lobes, devoid of trigones; lobe cells variable in shape and size; median cells very variable, quadrate and 38–42 μm to more often rectangulate and 19–30(36) μm wide × 52–76 μm long; basal cells oblong-hexagonal, 27–32 μm wide × 40–83 μm long; surface smooth or almost so in proximal half of leaf, in lobes finely but distinctly papillose. Oil-bodies lacking. Underleaves large, little or not wider than stem, about 0.55–0.65× area of lateral leaves, usually 15–18 cells broad (but often much smaller), broadly and transversely quadrate-reniform or rounded-oblong, 3–4-lobed to ca. 0.25–0.35; lobes few-celled (usually of 7–9, up to 16–20 cells), usually 1 or 2 lobes a little smaller, but not or weakly asymmetric, the lobes mostly terminating in 2 laterally juxtaposed cells, usually not ending in slime papillae. Asexual reproduction lacking.

Dioecious. Androecia on long or short, leafy branches, terminal but becoming intercalary, wider than vegetative axes (365–380 μm wide), very laxly spicate, usually more deeply pigmented than vegetative area; bracts in 2–6 pairs, remote, similar in size to leaves or barely larger, 2(3)-lobed, with erect to erect-incurved, acute lobes, from a suberect to obliquely spreading, strikingly concave, entire-margined base, the base semicircular in cross section; antheridia 1–2 per bract, nearly occupying the entire bract cavity, the stalk short, biseriate, the body spherical, formed of many irregular jacket-cells of small size; bracteoles distinct, clearly smaller than bracts, lingulate-ovate, a little concave, shallowly bifid, the short lobes usually incurved, lacking antheridia or (sometimes) monandrous. Gynoecia terminal on elongated but small-leaved axes or, more often, on rather abbreviated intercalary branches, arising (sometimes in juxtaposed groups of 3–4) indiscriminately in axils of lateral leaves and underleaves; bracts of innermost series 0.2–0.3(0.35) bifid, elliptical, the lobes acute, sometimes asymmetric, usually terminating in a single, tapered cell, the lobe margins entire; bracteole similar in shape and form, but a little smaller. Perianth fusiform, terete below, plicate in ca. distal half, narrowing to the contracted mouth, the mouth lobulate, the lobules each terminating in a single cell or a uniseriate row of 2 somewhat elongated, rather thin-walled cells, the terminal cell rounded at the summit and not sharp.

Capsule wall outer layer of cells with two-phase development, the longitudinal walls with obscure continuous sheets of secondary wall material and nodular to weakly extended thickenings, alternating with primary walls with thickenings absent or weakly developed.

Spores and elaters not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1370–1525 m), North Island (1240–1660 m).

A penalpine–alpine plant. In the alpine zone in mosaics of cliffs, outcrops and scattered alpine plants. In such situations it occurs over soil within crevices of boulders, outcrops and cliff faces, particularly where there are pockets or niches offering some degree of protection. It may be admixed with *Isotachis* or *Herzogobryum*. At times over soil between boulders in a streambed (Tongariro Natl. Park, Blyth Hut to Whakapapa Track, 1450 m). Also over soil between rocks at a creek margin in an exposed stream valley through penalpine scrub of *Halocarpus bidwillii*, *Ozothamnus leptophyllus* and *Phyllocladus alpinus* (Tongariro Natl. Park, Taranaki Falls Track, 1240 m). The type occurred admixed with *Hyalolepidozia* over peaty ground in the snow tussock (*Chionochloa*) zone.

Comments: This species is of particular interest since it possesses in varying degrees features usually regarded as diagnostic of *Hyalolepidozia* (normally only intercalary branching, both lateral and ventral), of *Paracromastigum* (the 2–3-lobed leaves and underleaves, the latter quite large, often approaching the leaves in size) and of *Pseudocephalozia* (the largest leaves and underleaves are relatively many-celled, the leaves 3-lobed on the most vigorous axes, the underleaves are often 4-lobed and the branching is intercalary from all 3 merophyte rows).

With substitution of intercalary for terminal, lateral branching, this species and *Paracromastigum drucei* are similar in branching modality to *Hyalolepidozia*. Also, in *P. fiordlandiae* the stem, with 8 large, inflated cortical cells, has an anatomy that approaches that of *Hyalolepidozia* (here cortical cells are in only 6 rows).

Paracromastigum fiordlandiae has an affinity to *P. drucei* in size and aspect, branching modes, leaf lobing and in the exceedingly remote leaves and underleaves. For differences between these species see the key.

The type of *Paracromastigum fiordlandiae* was described in Schuster and Engel (1996) as lacking perianths, and the small portion sent to Engel for study also lacked perianths. However, Schuster (2000a) illustrated both details of the gynoecium and sporophyte and the above description of these structures is based upon these figures.

Paracromastigum furcifolium (Steph.) R.M.Schust.

[Fig. 108: 1, oil-bodies, p. 469]

Cephalozia furcifolia Steph., Sp. Hepat. 3: 315. 1908. *Paracromastigum furcifolium* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 276. 1963. *Bonneria furcifolia* (Steph.) R.M.Schust., Nova Hedwigia 10: 24. 1965. Type: New Zealand, *Kirk 219 p. p.* ("inter Anthoc. 219") (G!).

Lepidozia cavernarum Herzog, Trans. & Proc. Roy. Soc. New Zealand 68: 44. *pl. 5, f. g–l.* 1938. Type: New Zealand, North Is., "Kiwi," Wairoa, Sept. 1931, *Hodgson 88.*

Plants usually pure green, at times clear yellowish white-green, somewhat water-repellent, small but not tiny, 550–960 μm wide. Branching markedly plastic: *Frullania*- and *Acromastigum*-type terminal branches typically present and frequent (but sparsely developed in some populations), *Microlepidozia*-type branches exceptional or sporadic; ventral-intercalary branches frequent; stoloniform branches rather common, long for plant size, nitid. Stems with cortical cells large and thin- or firm-walled, in 7–9 rows distinctly larger than the medullary cells, the cortical cells in surface view strongly elongated; medullary cells thin- or firm-walled. Main shoots with normally 2(3) elongate-rectangular cortical cells intervening between successive

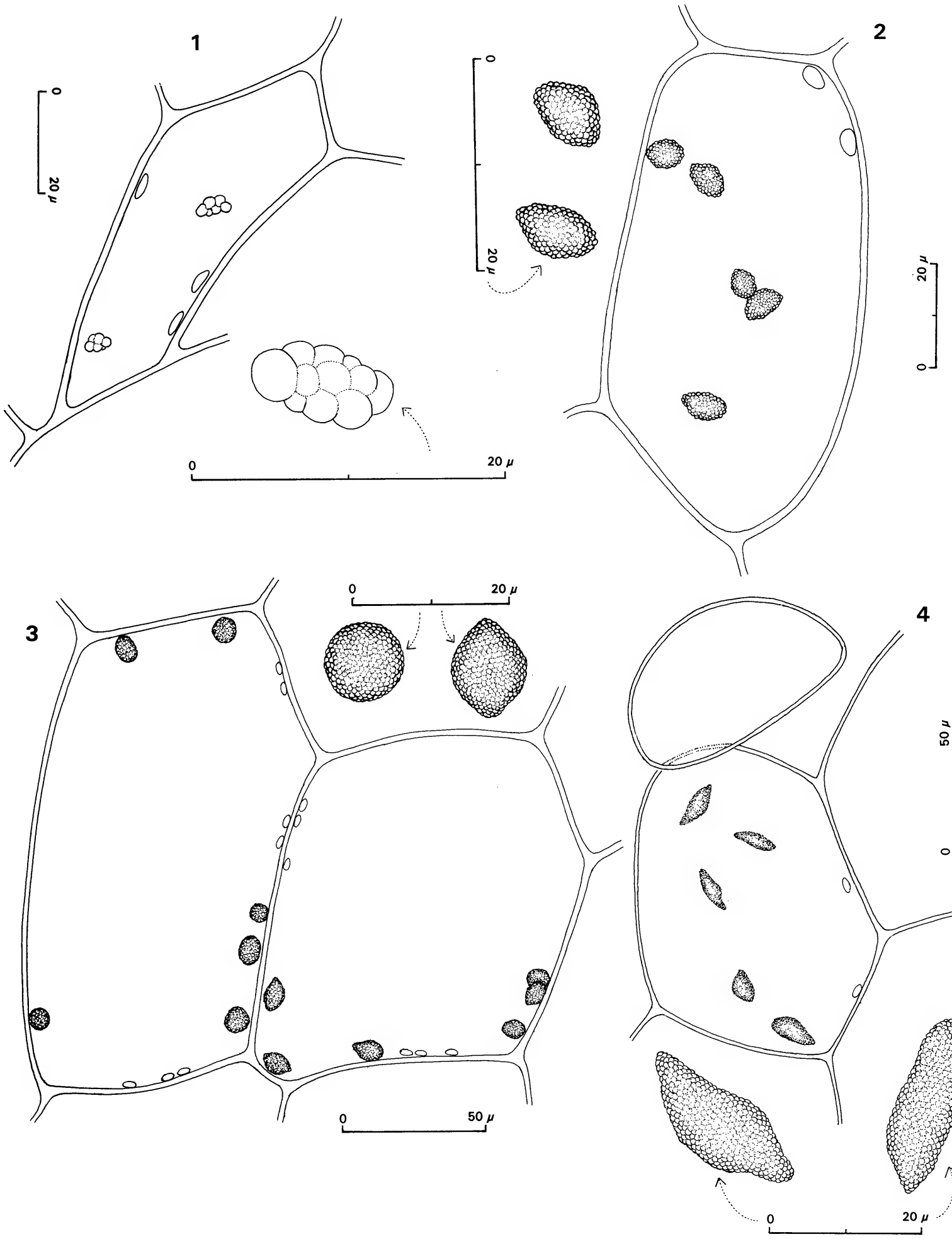

Fig. 108.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Paracromastigum furcifolium* (Steph.) R.M.Schust. Disc cell, below right an oil-body at higher magnification. 2. *Zoopsis macrophylla* R.M.Schust. Leaf cell, at left 2 oil-bodies at higher magnification. 3. *Zoopsis macrophylla* R.M.Schust. Stem cells, above 2 oil-bodies at higher magnification. 4. *Zoopsis leitgebiana* (Carrington & Pearson) Bastow. Basal cell of dorsal lobe, below 2 oil-bodies at higher magnification. (Fig. 1, from *Glenny 9597*, New Zealand, South Is., Western Nelson EP, Stockton Plateau; 2, 3, from *Glenny 8860*, New Zealand, South Is., Canterbury EP, Arthur's Pass, Margarets Tarn; 4, from *Glenny 9124*, New Zealand, South Is., Western Nelson EP, Mt. Burnett, near summit of Three Sisters.)

leaves on either side. Leaves rather rigid, at times subvertical, widely spreading, remote to contiguous, the insertion clearly succubous, not inserted to stem midline dorsally, most of the dorsal 2 cell rows leaf-free, 170–230 μm wide, 300–450 μm long, the leaves predominantly bifid or at times 2–3-lobed (the 3-lobed leaves have a longer dorsal lobe), the leaves divided to ca. 0.7–0.85; lobes lanceolate and rather acuminate, varying from 2 to 3–4 cells wide at base, terminating in a uniseriate row of 2–3 elongated cells; disc comprised of 1(2) tiers of cells along the insertion + the tier of laterally juxtaposed cells at the base of each lobe, the cells tending to lie in tiers, the disc 4–6 cells broad on bifid leaves, 6–7 cells wide on trifid ones. Cells of leaves clearly rectangulate, mostly 3–5:1, evenly rather firm-walled; surface of lobes finely striate-papillose, of disc finely striate or smooth. Oil-bodies inconspicuous and occupying a tiny portion of cell lumen, very pale grey, 1–3 per disc cell, irregularly elliptic, coarsely and distinctly botryoidal, with age and breakdown, the spheres coalesce and ultimately one large, smooth sphere ensues. Underleaves ca. 0.4–0.55× the leaves, 2–3-fid (majority of underleaves trifid on strong stems), the trifid underleaves nearly uniformly asymmetrical, with mostly 1 or 2 lobes reduced, 2–3-celled and ending in a slime papilla; disc 1 cell high, consisting of only the paired cells at the lobe bases or 1 or more cells may have transverse divisions, the disc then in part 1.5 cells high. Asexual reproduction frequent, by fragmentation of last 1–3 cell tiers of leaf lobes.

Androecia on short (but not abbreviated) ventral-intercalary branches from leafy shoots or arising from microphyllous creeping axes, the branches may initially produce 1 or a few gyres of distant, reduced, bifid leaves, the androecia exceptionally very long-spicate and lacking normal sterile leaves, with the bracts in up to 18 pairs, the androecial branches at times producing a weak ventral-intercalary branch and (even on the same androecial branch) an *Acromastigum*-type leafy branch; bracts at times pale brown distally, a little dorsally assurgent, bifid, the disc moderately ventricose; bracteoles much smaller, flat, bifid; antheridia 1 per bract, the stalk biseriate. Gynoecia on short ventral-intercalary branches; bracts of innermost series much larger than leaves, bifid to 0.45; lobes mostly terminating in a uniseriate row of 2–3 cells, the lobe margins with a few teeth; disc margins sparingly crenulate by projecting upper ends of cells, + small teeth also present; bracteole basically similar to bracts but a little smaller. Perianth mouth lobulate, the lobules terminating in a uniseriate row of 2–3 somewhat elongated cells, the terminal cell rounded at the summit; perianth unistratose but locally bistratose toward base.

Capsule wall 2–3-stratose.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (near sea level), South Island (0–700 m), North Island (10–1035 m). Known from Westland, Western Nelson, Southern North Island, Volcanic Plateau, Auckland and Northland EPs.

A rather common species with a broad range, extending from Stewart Island to Northland, but uncommon in the South Island. The species typically occurs in felt-like mats over raw sandy or clayey soil of banks, particularly steep and vertical banks that may or may not be associated with streams. The banks may be within the forest and at times rather heavily shaded, or they may be relatively well illuminated, such as at roadsides, sometimes under light shade of tall ferns such as *Blechnum novae-zelandiae*. A characteristic niche for the species is that of the concave portion of the lip at the upper extreme of vertical banks, the lip usually formed by the forest edge above. For example, at Stockton Plateau (700 m) it was found on the sloping roof of a rock overhang above a stream, with *Acromastigum colensoanum*, *Telaranea inaequalis*, *Zoopsis bicruris* and *Z. setulosa*. In open sites it has been found with *Drucella integristipula*, *Fissidens asplenioides*, *F. pallidus*, *Jackiella curvata* and *Leucobryum candidum*, while in

more shaded forest sites it occurs with *Acromastigum colensoanum*, *Lepidozia spinosissima*, *Psiloclada clandestina*, *Saccogynidium australe* and *Zoopsis setulosa.*

Also over wet soil in a wet, poorly drained bog with the margin dominated by *Leptospermum*, with some *Calluna vulgaris* (near Tawhai Falls Track, Tongariro Natl. Park, 1035 m). Also over wet soil, with sedges and *Gleichenia* in an ecotonal area of *Typha orientalis* swamp and *Leptospermum scoparium* swamp (ca. 10 m, track to Te Werahi Beach, directly south of Cape Reinga).

Paracromastigum macrostipum (Steph.) R.M.Schust.

Cephalozia macrostipa Steph., Hedwigia 32: 315. 1893. *Paracromastigum macrostipum* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 276. 1963. *Pseudocephalozia macrostipa* (Steph.) R.M.Schust., Nova Hedwigia 10: 21. 1965. Type: New Zealand, Tauranga, *Kirk 113 – c. per.* (G!).
Cephalozia kirkii Steph., Sp. Hepat. 3: 314. 1908, *syn. fide* Schuster (2000a, p. 374). *Paracromastigum kirkii* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 276. 1963. Type: New Zealand, Tauranga, *Kirk 407– c. sporo.* (G!)

Plants creeping to ascending, green in shade phases, with exposure developing reddish brown pigments, 310–600 μm wide, the basal portion often creeping, whitish, microphyllous and flagelliform prior to becoming leafy, the leading leafy shoots often broadly arching. Branching common, the branches ascending, frequently of *Acromastigum* type, occasionally of *Frullania* type; *Microlepidozia*-type branches lacking; ventral-intercalary branches abundant. Stems with cortex firm-walled, much larger than the thin- to weakly firm-walled medullary cells, the stems with 10–11 rows of cortical cells + 8–10 rows of medullary cells varying to 6–7 cortical cells + 5–6 medullary cells. Rhizoids at underleaf bases. Main shoots with 2–3 elongate-rectangular cortical cells intervening between successive leaves on either side. Leaves vertical, rather strongly dorsally assurgent, suberect, imbricate, the insertion succubous (at times feebly so), not inserted to stem midline dorsally, at least part of the dorsal 2 cell rows leaf-free, the leaves 300–360 μm wide × 400–480 μm long, bifid or (frequently) trifid, the leaves divided to ca. 0.45–0.55; lobes acute, 4–6 cells wide at base, terminating in a single isodiametric cell or a uniseriate row of 2 subisodiametric cells, the tip cell rather broadly rounded at the summit; disc 2–4 cells high, the basal tier tending to be larger, or at least longer, the disc 10–14 cells wide. Cells feebly, equally firm-walled, the median disc cells 22–30 μm wide × 37–54(60) μm long; surface weakly striate-papillose. Oil-bodies present in some cells, especially toward the base of the disc, occupying a tiny fraction of the cell, hyaline, glistening, 2–3 per basal disc cell, conspicuously botryoidal, the spherules very quickly swelling and coalescing. Underleaves ca. 0.45–0.5× the leaves, 2–3-fid to ca. 0.5, the lobes asymmetrical, with 1 or 2 lobes smaller and ending in a slime papilla; disc 3 cells high.

Plants dioecious. Androecia not seen. Gynoecia with bracts of innermost series much larger than leaves, bifid to 0.4–0.45; lobes terminating in a uniseriate row of 3 cells, the lobe margins with up to 4 strong teeth and at times an accessory lobule; disc margins with a few small teeth; bracteole similar to bracts but a little smaller. Perianth long-exserted, trigonous, somewhat but not strongly narrowed to the mouth, the mouth dentate-ciliolate, the teeth discrete from one another and terminating in a single cell or a uniseriate row of 2 somewhat elongated cells, the terminal cell rounded at the summit.

Capsule wall 2-, locally 3-stratose; outer layer of cells with sharply defined two-phase development, the longitudinal walls with continuous sheets of secondary wall material and

strong nodular thickenings, alternating with primary walls with thickenings absent; inner layer of cells with a few to several semiannular bands and (commonly) nodular thickenings.

Spores and elaters not seen.

Distribution and Ecology: Endemic to New Zealand: North Island (405–480 m). Known only from Auckland and Volcanic Plateau EPs.

Known only from a few collections: the type locality at Tauranga (Bay of Plenty), the Kaimai Ra. (spur ESE of Ngatamahinerua, headwaters of Poupou Stream, 405 m), Kaingaroa Plain near Waiotapu and Utuhina Stream west of Rotorua (ca. 450 m) as well as the Old Kaimai Road. At the Kaimai Ra. site the species was found on bare clay of a drainage channel in a stream valley under an open canopy of *Beilschmiedia tawa* and *Weinmannia silvicola*; subcanopy dominants were *Schefflera digitata*, *Cyathea dealbata* and *C. smithii*, and a shrub layer consisted of *Freycinetia baueriana* and *Cortaderia*. Locally common at Old Kaimai Road (boundary of Kaimai-Mamaku Forest Park, 460–480 m) on roadside clay banks as well as the raised roadside clay bed. At the Utuhina Stream site it was found "on a bank in bush" with *Solenostoma inundatum*, *Campylopus clavatus* and *Isotachis montana*. Schuster (2000a) recorded the species from Tongariro Natl. Park. The species apparently is restricted to exposed fine-grained soils.

Comments: Plants of this species have a superficial resemblance to *Cephalozia*, but may be immediately distinguished from that genus by the presence of well-developed underleaves, which are up to 0.5 the leaf size, the position of rhizoids at underleaf bases and the frequent trifid leaves.

Paracromastigum macrostipum may be distinguished from the other member of subgenus *Austrocephalozia* in our area, *P. furcifolium*, by the presence of reddish brown pigments, the rather densely imbricate leaves, with acute lobes that terminate either in a single cell or a uniseriate row of 2 subisodiametric cells and the higher underleaf disc (3 cells high).

Oil-bodies appear to behave very similar to those of *Paracromastigum furcifolium*. In both species oil-bodies are present only in some cells, inconspicuous, up to 3 per cell and conspicuously botryoidal. Also, oil-body breakdown in both species is similar, with spherules very quickly swelling and coalescing.

Hyalolepidozia S.W.Arnell *ex* Grolle

Hyalolepidozia S.W.Arnell *ex* Grolle, Rev. Bryol. Lichénol. 32: 179. 1964 (1963). *Hyalolepidozia* S.W.Arnell, Bot. Not. 115(2): 203. 1962, *nom. inval.*, *sin. descr. lat.*

Plants anisophyllous, soft, creeping, whitish to pale green, lacking secondary wall pigments, very small. Branching irregular, the branches nearly exclusively lateral-intercalary and less commonly, ventral-intercalary; creeping or geotropic stolons developed; terminal branching very rare, of *Frullania* and *Microlepidozia* types. Stems delicate, soft and rather fleshy, the cortex in 6(7) rows of very large, inflated cells with thin to only weakly thickened walls, forming a conspicuous hyalodermis; medullary cells much smaller, in 8–13 rows, strongly elongated. Rhizoids at underleaf bases. Leaves remote to sporadically contiguous, the insertion transverse to weakly or distinctly incubous, the insertion extending to stem midline dorsally or virtually so, the orientation at times transverse (the leaves then vertical); leaves concave, composed of relatively few cells, nearly uniformly bilobed to 0.45–0.65 (leaves sporadically

3-lobed in *Hyalolepidozia microphylla*), the lobes narrowly acute, 3–4 cells wide at base, terminating in a single cell or a uniseriate row of 2–3 cells; disc typically 2–4 cells high. Cells of leaves mostly oblong, thin-walled to feebly thick-walled, lacking trigones; surface smooth or delicately papillose. Underleaves much smaller than leaves, bilobed or, if asymmetrically 3-lobed (rare), then with 1–2 of the lobes reduced; disc usually 1–2(3) cells high. Asexual reproduction lacking.

Dioecious or autoecious. Androecia on short lateral- and ventral-intercalary branches, subspicate; bracts concave, bifid to ca. 0.5; antheridia 1 per bract, the stalk biseriate; bracteoles lacking antheridia. Gynoecia on short lateral- and ventral-intercalary branches; bracts of innermost series much larger than leaves, 2(3)-dentate or lobed up to 0.45; lobes terminating in 2 laterally juxtaposed cells, a single cell or a uniseriate row of 2 cells, the lobe margins entire or with a few teeth toward base; disc margins entire or with a few small teeth or irregularly crenulate by projecting upper ends of cells, at times with a lobule near base of 1 or both main lobes; bracteole similar to bracts. Perianth long-exserted, fusiform to linear, terete below, trigonous above, narrowing to the not or contracted mouth, the mouth lobulate, the lobules each terminating in a single cell or the summit crenulate by cells laterally free for varying distances, the terminal cells somewhat elongated, rounded at the summit and not sharp.

Seta with 8 rows of large outer cells and 13 rows of much smaller internal cells. Capsule wall 2- or 3-stratose; outer layer of cells with two-phase development, the primary walls lacking pigmented thickenings, the secondary walls with thin continuous sheets of pigmented wall material and with nodular thickenings present and low or only feebly developed, lending the walls a sinuous appearance; inner cells with nodular to feebly extending thickenings common, with a few complete semiannular bands.

Spores with low but sharply defined, close papillae and short, simple or at times furcate vermiform ridges that at times anastomose; spore:elater diam. ratio 1–1.2:1. Elaters rather rigid, short, only 91–142 μm long, bispiral.

Type: *Hyalolepidozia bicuspidata* (C.Massal.) S.W.Arnell *ex* Grolle (≡ *Lepidozia bicuspidata* C.Massal.)

A genus of two species. *Hyalolepidozia bicuspidata* (C.Massal.) S.W.Arnell *ex* Grolle is amphi-Atlantic-temperate, occurring in South Africa, Table Mtn., Falkland Islands (see Engel, 1990a), southern South America (see Engel, 1978), Juan Fernandez and "Frai Jorge" (northern Chile). A second species occurs in New Zealand. *Hyalolepidozia longiscypha* (Taylor) Grolle of western Australia was transferred to *Paracromastigum* by Schuster and Engel (1996).

Reference: Schuster (2000a).

Hyalolepidozia microphylla R.M.Schust. *ex* J.J.Engel

[Fig. 109]

Hyalolepidozia microphylla R.M.Schust., Beih. Nova Hedwigia 118: 387. *f. 155*, *156*. 2000, *nom. nud.*, *sin. descr. lat. Hyalolepidozia microphylla* R.M.Schust. *ex* J.J.Engel, Novon 17: 310. 2007. Holotype: New Zealand, South Is., Fiordland, Hunter Mtns., Mt. Burns, 4500–5000 ft., *Schuster 84-101b* (herb. Schuster).

Plants soft-textured, delicate and filiform, but rather fleshy, highly nitid and glistening, light to whitish green, minute. Branching copiously produced below, uniformly intercalary, with

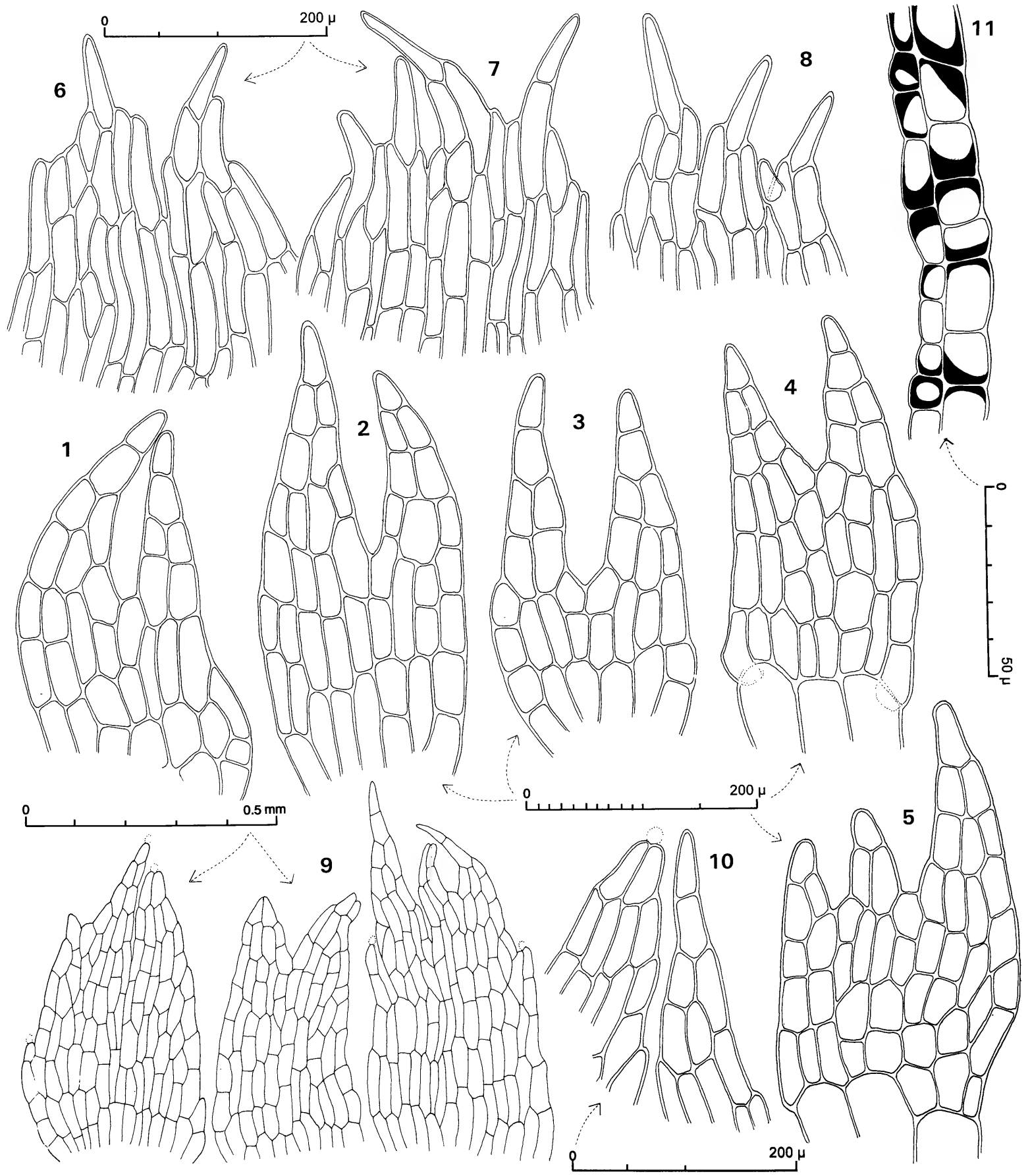

Fig. 109.
Hyalolepidozia microphylla R.M.Schust. *ex* J.J.Engel. 1–5. Leaves. 6–8. Portions of perianth mouth. 9. Bracts, and in middle, bracteole from mature, sporophyte-bearing gynoecium. 10. Two lobes of innermost ♀ bracts. 11. Capsule wall, cross section. (All from *Engel 21453*, New Zealand, South Is., Sounds–Nelson EP, Mt. Richmond Forest Park, Red Hills, track to Maitland Hut.)

both ventral- and lateral-intercalary branches common, the branches forming a system of ramified, creeping or geotropic, microphyllous stoloniform axes, or becoming ascending to erect and leafy, the leafy axes simple or sparingly branched. Stems with cortical cells large, inflated, thin- to slightly firm-walled, in 6(7) rows, in surface view short-oblong; medullary cells much smaller, in 8–13 rows. Rhizoids frequent, at bases of most underleaves and leaves of creeping

axes, the tips often dilated and bulbous but never ramified. Main shoots with usually 4–6 cortical cells intervening between successive leaves on either side. Leaves remote, vertically oriented, at times weakly falcate, rather obliquely spreading, transverse to feebly incubous, inserted to stem midline dorsally, oblong-ovate, 120–135 μm wide × 215–250 μm long to 160–180 μm wide × 270–320 μm long; leaves bifid to 0.55–0.65, mostly subequally bifid, or, less often, the ventral lobe somewhat smaller or abbreviated and ending in a slime papilla, 3-fid leaves occasionally present, these always with an abbreviated ventral lobe terminated by a slime papilla; lobes narrowly acute, (2)3–4 cells wide at base, terminating in a single cell or a uniseriate row of 2 cells, the tip cell of lobe slightly longer than wide and weakly tapering to a rounded summit; disc 2–3.5 cells high, 6–8 cells wide. Cells of disc weakly firm-walled, 15–18 μm wide × 50–60 μm long to (18)20–26(28) μm wide × 36–67(72) μm long; surface of lobes delicately papillose at least at apices, of disc faintly striate-papillose or smooth. Underleaves variable in size and form, narrower than stem, usually less than 0.55× area of leaves (on some shoot apices to 0.85 as large), remote, 2(3)-fid, when 3-fid often with 1–2 lobes aborted, the aborted lobes consisting of 1–3(4) cells and ending in a slime papilla; disc usually 2 cells high, 6–7 cells wide.

Plants dioecious, the androecia and gynoecia often in close proximity. Androecia mostly on ascending or erect branches of limited length; bracts contiguous to imbricate, moderately larger than leaves, concave, bifid to ca. 0.4; antheridia 1 per bract, the stalk biseriate; bracteoles lacking antheridia. Gynoecia on very short lateral-intercalary branches usually without or sporadically with 1–2(3) cycles of vegetative leaves prior to bract formation; bracts of innermost series ovate to obovate, 2(3)-lobed to 0.45, the lobes terminating in 2 laterally juxtaposed cells, a single cell or a uniseriate row of 2 rather elongate cells (to 3:1), the margins entire or with a 1-celled tooth, the disc margins entire or with a low blunt tooth formed by projecting upper ends of cells; bracteoles 2-lobed, much like bracts but slightly smaller. Perianths long-exserted, linear to long-fusiform, to 2500 × 300 μm (to 8.3:1), frequently arched, terete at base but trigonous in distal 0.6 or more (at times trigonous into the basal sector), tapering to the not or weakly contracted mouth, the mouth 9-lobulate, the lobules each comprised of a tier of 3–6 laterally juxtaposed, elongate cells occasionally followed by a second tier of 2 laterally juxtaposed elongate cells, the lobules then each terminating in an elongate, firm-walled cell (20–23 × 72–100 μm) that gradually tapers to a rounded summit; perianth 6-stratose toward base.

Seta extending capsule far beyond perianth, seen only in collapsed state (the seta collapsed even when sporophyte surrounded by perianth). Capsule long-ellipsoidal to linear, the walls exceedingly delicate and easily fragmenting, 17–19 μm thick, 2-stratose, the outer layer to ca. 2× the thickness of inner layer; outer layer of cells with two-phase development, the primary walls lacking pigmented thickenings, very delicate, with exposed tangential wall thin, the cells apparently rather soon collapsing, the secondary walls with thin continuous sheets of pigmented wall material and low nodular thickenings; inner layer of cells markedly long and narrow, with continuous sheets of pigmented wall material, the radial walls with strong nodular thickenings that often feebly extend onto the outer tangential wall, with complete, rather wide, semiannular bands sometimes present.

Spores 13.4–14.4 μm in diam., the spore wall red-brown, thin, with low but sharply defined, close papillae and short, often curved, simple or at times furcate vermiform ridges that at times anastomose but do not form areolae; spore:elater diam. ratio 1–1.2:1. Elaters rather rigid, 11.5–13.4 μm wide, short, only 91–142 μm long, tapered to the tips, bispiral to tips, the spirals 3.8–4.8 μm wide, closely wound.

Distribution and Ecology: Endemic to New Zealand: South Island (700–920 m), North Island (1450 m).

Known from only a few sites. In Tongariro Natl. Park (Blyth Hut to Whakapapa Track) plants occurred over soil of a recess under a rock overhang at 1450 m in the alpine zone. Also over soil under partial rock cover in a rather open *Leptospermum scoparium* scrub forest in a serpentine area (Red Hills, Mt. Richmond Forest Park, ca. 700–920 m). Plants occur in interwoven, diffuse patches. Schuster (2000a, p. 387) stated that the species occurs in "alpine moorlands of Fiordland."

Comments: This minute, thread-like plant differs from the type of the genus, *Hyalolepidozia bicuspidata* as follows:

Key to species of *Hyalolepidozia*

1a. Leaf lobes terminating in a single cell; leaves sporadically 3-lobed; perianth mouth lobules each comprised of a tier of 3–6 laterally juxtaposed cells occasionally followed by a second tier of 2 laterally juxtaposed elongate cells, the lobules then each terminating in a single cell; capsule wall 2-stratose; plants dioecious . . . . . *H. microphylla*

1b. Leaf lobes terminating in a uniseriate row of 2–3 cells; leaves always bifid; perianth mouth lobules each with several (to 4) tiers of laterally juxtaposed cells subtending a single cell or with the lobule summit crenulate by cells laterally free for varying distances; capsule wall 3-stratose; plants autoecious (?always) . . . . . *H. bicuspidata*

The species can easily be confused with *Paracromastigum fiordlandiae*, which is rather similar in size and has nearly exclusively intercalary branches that also originate from all three rows of merophytes. Since the two may be confused, a key is provided here to distinguish them:

1a. Stem consistently with 6(7) rows of very large, hyaline cortical cells; leaves usually symmetrically 2-fid (sporadically 3-fid), the dorsal lobe 2–4 cells wide at base; main shoots usually with 4–6 cortical cells intervening between successive leaves on either side . . . . . *H. microphylla*

1b. Stem with cortex in (8)9 rows, occasionally ranging to 12 rows; leaves usually asymmetrically 3-lobed, the dorsal lobe largest, 5–9 cells wide at base; main shoots usually with 6–8 cortical cells intervening between successive leaves on either side . . . . . *P. fiordlandiae*

Paracromastigum drucei also is a minute plant with rare production of terminal branches, but that species differs from *Hyalolepidozia microphylla* in the brownish pigmentation (at least in exposed sun forms), the 2–3(4)-lobed leaves and the cortical cells in 9–12 rows.

The species is illustrated in Schuster (2000a, figs. 155, 156); figures show only young gynoecia. *Engel 21453* (Sounds–Marlborough EP, Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, 700–920 m) has mature sporophytes. Gynoecial and sporophyte characters were derived from this specimen (see also Fig. 109).

Zoopsis Hook.f. *ex* Gottsche, Lindenb. & Nees

Zoopsis Hook.f. *ex* Gottsche, Lindenb. & Nees, Syn. Hepat. 473. 1846.

Plants closely creeping or adnate, often in interwoven thin patches, pellucid, pale to pure green, nitid when dry, small to very small, usually less than 800 μm wide. Branching sparing to common, irregular, the branches terminal, of *Frullania* (with half-leaf) and *Zoopsis* types (lacking a half-leaf) and ventral-intercalary; geotropic, subterete, microphyllous, pale, ventral-intercalary flagella (or extensions of leafy axes) typically common. Stems typically strongly flattened and gradually merging into the reduced leaves, in cross section planoconvex or, in a few taxa, subterete or elliptical; cortical cells normally in 6 rows (8–9 rows in a few taxa), the cells in the dorsal and lateral rows exceptionally large, inflated and pillow-like, forming a distinctive hyaloderm, the ventral 2(3) rows of cortical cells smaller, often conspicuously so, the cortical cells in surface view rather short, often in a zigzag arrangement like the scales of a reptile; medullary cells much smaller, numerous, forming a well-defined central conducting strand, the cells in surface view strongly elongated. Rhizoids infrequent to frequent, from bases of underleaves and at times from bases of lateral leaves, the tips often swollen and dendritic. Leaves variable, basically bilobed and with the insertion succubous (nearly longitudinally attached to lateral margins of axis), in a few taxa many-celled, with a distinct, many-celled disc, the lines of insertion extending nearly to dorsal stem midline, or (more commonly) in other taxa the insertion not extending to stem midline and then defining a continuous leaf-free dorsal strip of 2 rows of cortical cells; leaves in some species rudimentary and 4–6-celled, consisting of 2 basal cells and 2 "lobes" each formed of 1 or 2 specialized, curved, chlorophyll-free, papilliform cells, or the leaves reduced to ephemeral slime papillae. Cells leptodermous, usually inflated and pillow-like, subisodiametric, extremely large, 45–65 × 60–95 μm or even larger, the leaf and cortical cells of similar size; surface smooth. Oil-bodies several to many per cell, granular-botryoidal or finely granular-botryoidal (nearly smooth in *Z. caledonica*). Underleaves present throughout, inconspicuous, very small, comprised of up to ca. 12 cells or, more commonly, vestigial and comprised of 2–4 subspherical basal disc cells + a pair of 1-celled lobes each terminating in a slime papilla. Asexual reproduction lacking or by fragmenting or caducous leaf lobes (*Z. ceratophylla*, *Z. matawaia*) or by tubers (rarely in *Z. leitgebiana*).

Dioecious. Androecia on abbreviated, ventral-intercalary branches; deeply concave to ventricose and with a demonstrable disc, the apices bilobed; antheridia 1 per bract, the stalk 1- or 2-seriate. Gynoecia triradial, on abbreviated, ventral-intercalary branches; bracts of innermost series 2(3)-lobed from 0.6 to nearly to the base; lobes narrow, often with a few to several biseriate tiers, terminating in a single cell or a uniseriate row of 2–6 cells, the lobe margins entire or with a tooth; disc 2–5 cells high, the margins entire or with a tooth; bracteole similar to bracts or a little smaller. Perianth trigonous-fusiform, mouth deeply 6-lobed to ca. 0.5 in most species, the lobes narrow, with a few to several biseriate tiers, terminating in a uniseriate row of up to 6 often moniliform cells or, occasionally, a pair of laterally juxtaposed cells, the lobe margins entire, or (*Zoopsis ceratophylla*) the mouth lobed a small fraction of perianth length, the lobes caudate, each terminating in a cilium or (*Z. bicruris*) the mouth unlobed and dentate.

Seta with 8 rows of outer cells surrounding an inner core of 10–21 rows of small cells. Capsule ellipsoidal, yellow-brown and without red-brown pigments, wall 2- or (*Zoopsis leitgebiana*) 2–3-stratose; outer layer of cells with modified two-phase ontogeny, with primary walls lacking pigmented thickenings or nearly so, the secondary walls all (longitudinal + at times also transverse) with continuous sheets of brown or yellow-brown pigmented wall material +

irregular nodular to weakly extending thickenings lending the walls a sinuous appearance; inner layer of cells short to narrowly long-rectangular, with narrow, yellow-brown semiannular bands, the bands usually complete, often incomplete.

Spores delicately areolate. Elaters straight or nearly so, hardly tapering toward the tips, bispiral.

Type: *Zoopsis argentea* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees (≡ *Jungermannia argentea* Hook.f. & Taylor)

A genus of 10 species, all of which are Old World. The center of diversification of the genus is evidently Australasia, with all three subgenera represented there. All subgenera (*Amphizoopsis* R.M.Schust., *Eozoopsis* R.M.Schust. and *Zoopsis*) occur in New Zealand, together with all but two species. *Zoopsis setigera* K.I.Goebel ranges from West Irian and Papua New Guinea and the Solomon Islands to Indonesia (Molucca Islands, Amboina) to Borneo (Grolle and Piippo, 1984). *Zoopsis liukiuensis* Horik. ranges from Queensland, New Guinea, New Caledonia, Solomon Islands and Samoa to the Moluccas, Indonesia (Java, Sumatra, Amboina), Borneo, Malaysia, Philippines, Taiwan, Liukiu Island and Kyushu in southernmost Japan (Grolle and Piippo, 1984). The genus is lacking in south temperate and tropical America and from Africa.

Zoopsis is appropriately named, the type species and those immediately allied to it have very large, pillow-like, polygonal cortical cells that evoke a curiously "reptilian" appearance. Species like *Z. argentea*, and in particular the var. *flagelliformis*, have evolved what appear to be linear thalli, the leaves reduced to vestiges that form mere scallops on the margins of the flattened "frond." The remarkable *Z. nitida* has leaves reduced to ephemeral slime papillae. However, the more primitive species (subg. *Eozoopsis*, subg. *Amphizoopsis*) retain leaves with a distinct lamina. The genus includes several of the most extraordinary hepatics found anywhere. They show progressive flattening of the axis and the coalescence of the flattened axis and rudimentary leaves into a ribbon-like "frond" that simulates a thallus.

References: Glenny et al. (1997); Renner et al. (2006); Schuster (1993, 1999a, 2000a); Scott (1969).

The following key and treatment of taxa are adapted, with considerable modification, from Schuster (1999a).

Key to Species

1a. Plants with well-defined leaves, the lamina distinct, of ca. 4 or more cells broad, the leaves obviously bilobed (at least the ventral lobe several-celled); lobes formed of several moniliform cells, the terminal cell never papilliform 2

2a. Leaves symmetrically bilobed, rectangular, contiguous, the disc several cells high, the leaf orientation subhorizontal 3

3a. Shoots with an uneven, raggedy appearance due to caducous leaf lobe apices; leaf lobes longer, acuminate, terminating in a uniseriate row of (2)3–5(7) moniliform cells, the terminal cell at times ending in a slime papilla; leaves narrowly oblong to obovate-cuneate, often widest in the distal half, the lobes often somewhat spreading; oil-bodies opaque, brownish grey, finely granular; lobes of perianth mouth each with a contorted cilium to 8.5:1, the cilia

subtended by 2 laterally juxtaposed markedly elongated cells; seta with 8 rows of outer cell rows and numerous, much smaller internal cells; plants dioecious. Subg. *Amphizoopsis* . . . . . *Z. ceratophylla* (p. 484)

3b. Shoots with a crisp, regular appearance, the leaf lobes always persistent; leaf lobes few-celled, acute, nearly always terminating in a uniseriate row of 2 cells, the terminal cell never ending in a slime papilla; leaves narrowly oblong-lingulate, consistently tapered to the subparallel lobes; oil-bodies glistening, hyaline, smooth and homogeneous or nearly so; lobes of perianth mouth each with a stiff, noncontorted cilium to 6:1, the cilia subtended by 2–4 laterally juxtaposed cells that are ca. 2:1 or less; seta with 8 outer rows and 4 rows of similar-sized internal cells; plants autoecious . . . . . [*Zoopsidella caledonica*, p. 496]

2b. Leaves strongly asymmetrically bilobed, remote, the disc 1–2 cells high, the leaf orientation oblique. Subg. *Eozoopsis* 4

4a. Underleaves well developed, comprised of 12–15 cells, with 2–3-celled lobes, the underleaves separated by ca. 7–8 tiers of ventral cortical cells; leaves separated by 4–7 cortical cells on each side of axis; ventral lobes many-celled, the dorsal comprised of up to 8 cells; half-leaf 2–4 cells wide at base, followed by 1–2 biseriate tiers and a uniseriate row of 2–3 cells; stem with cortical cells in 7–8 rows, the medullary in 18–25 rows . . . . . *Z. macrophylla* (p. 480)

4b. Underleaves rudimentary, few-celled: the lobes of 2 cylindrical cells + terminal papillae, arising from 2–3 small spherical cells, the underleaves normally separated by 2–3 tiers of ventral cortical cells; leaves separated by 1.5–3(4) cortical cells on each side of axis; ventral lobes (4)5–8-celled, the dorsal 2–3-celled; half-leaf normally uniseriate throughout; stem with cortical cells in 6 rows, the medullary in 12–16 rows . . . . . *Z. leitgebiana* (p. 481)

1b. Plants with leaves rudimentary, formed of 4–6 cells or (*Z. nitida*) reduced to ephemeral slime papillae. Subg. *Zoopsis* 5

5a. Mature shoots with leaves reduced to 2 large, chlorophyllose basal cells (broadly united to and co-extensive with axis), or (*Z. matawaia*) consisting of 2 uniseriate lobes, with the basal cell of each lobe partially united; shoots uneven, the lateral margins interrupted by the leaf rudiments 6

6a. Leaves comprised of 2 uniseriate lobes, the terminal cell not capped by a hyaline papilla; asexual reproduction by readily fragmenting leaf lobes . . . . . *Z. matawaia* (p. 485)

6b. Leaves not organized into uniseriate lobes, the leaves each with apical, persistent papillae; asexual reproduction lacking 7

7a. Leaves formed by 2 projecting chlorophyllose basal cells, each with a falcate or hooked, conspicuous, roughened, 2-celled appendix that is attached by the narrow base of the basal cell; leaf rudiments juxtaposed, less than one-half of a cortical cell between leaf bases . . . . . *Z. setulosa* (p. 494)

7b. Leaves formed by 2 projecting chlorophyllose basal cells, each terminating in a crescentic, smooth, 1-celled papilla that is attached by its longer side; leaf rudiments separated by intervals formed by more than a full cortical cell . . . . . *Z. argentea* (p. 488)

5b. Mature shoots with leaves present but vestigial and at times disappearing in older parts of the shoot (*Z. bicruris*) or the shoots altogether devoid of chlorophyllose leaves, the shoot apices with ephemeral, hyaline, unicellular vestiges (+ a rudimentary papilla at anterior edge); shoots vermiform, the lateral margins of axis smooth or nearly so at maturity 8

8a. Terminal branches lacking, branching strictly ventral-intercalary; shoot apices clavate, abruptly narrowing to an acute tip; leaves not ephemeral and often present in older parts of the shoot, bifid, consisting of 4 cells: 2 basal cells (the "disc"), each with 1 large and conspicuous ovoid cell (the "lobes"); perianth mouth unlobed, dentate by 1–2-celled teeth . . . . . *Z. bicruris* (p. 491)

8b. Terminal branches present; shoot apices not clavate and narrowing at the tip; leaves ephemeral, visible only at shoot apex, usually a mere thin-walled, spur-like, hyaline, solitary cell; perianth mouth lobed to ca. 0.5 . . . . . *Z. nitida* (p. 492)

Zoopsis macrophylla R.M.Schust.

[Fig. 108: 2, 3, oil-bodies, p. 469]

Zoopsis macrophylla R.M.Schust., Nova Hedwigia 68: 14. *f. 1: 9–14*. 1999 ("*Zoopsisma crophylla*"). Holotype: New Zealand, South Is., Westland, bog N of Omoeroa River, town of Franz Josef, *Schuster 67-247* (herb. Schuster).

Plants markedly soft-textured, lax, creeping, pale to whitish green, nitid when dry, relatively vigorous, to 1.6 mm broad. Branching freely but rather remotely 1-pinnate, the branches of *Frullania* type; half-leaf lanceolate, comprised of many inflated cells, 2–4 cells wide at base, followed by 1–2 biseriate tiers and a uniseriate row of 2–3 cells; ventral-intercalary stoloniform branches occasional. Stems terete, pellucid, the cortical cells in 7–8 rows: the dorsal in 2 rows of exceedingly large, inflated cells, the lateral in 2–3 rows of cells similar in size to the dorsal, the ventral in 2–3 cells rows of smaller cells; medulla of 18–25 rows of small cells; dorsal cortical cells in surface view subquadrate to short-rectangular, leptodermous. Rhizoids few on leafy axes, frequent on stolons from bases of all appendages. Leaves remote, with 4–7 cortical cells intervening between successive leaves on each side of axis; leaves succubously inserted, the insertion nearly reaching the dorsal stem midline (ca. 0.5 of dorsal-most cortical cell leaf-free on each side), the leaves relatively large, strongly asymmetrical, 500 × 250 μm to 700–725 × 350–400 μm, asymmetrically bifid to over 0.65; lobes spreading but tips often incurved, the lobe apices each terminating in a uniseriate row of submoniliform, progressively smaller, persistent cells, the tips never with a differentiated papilla, the dorsal lobe smaller, mostly 4–8-celled, uniseriate for distal 3–4 cells, the ventral lobe lanceolate, 2–4 cells wide at base × 6–9 cells long; disc 1 cell high × 4–6 cells wide. Cells of leaves very large, leptodermous, inflated, at lobe bases 70–100 × 100–130 μm; surface smooth. Oil-bodies very small in proportion to cell volume, appearing distant and isolated in cell, grey, 4–5 per leaf cell, 6 per cortical cell, coarsely papillose, subglobose to elliptic to flask-shaped. Chloroplasts large for cell size. Underleaves distinct, separated by ca. 7–9 tiers of ventral cortical cells, small to relatively large, the lobes discrete, 1–2 cells wide and 2–3 cells long, the larger underleaves 250–290 μm wide × 240–260 μm long, with disc 4 cells wide and 1–2 cells high. Asexual reproduction absent.

Dioecious. ♂ Bracts relatively few-celled, bifid, concave; antheridial 1 per bract, the stalk uniseriate. Gynoecia with bracts oblong to obtrapezoidal, bifid to 0.7, the lobes acute to short-acuminate, terminating in a single cell or a uniseriate row of 2(3) cells, the lobe margins entire or often with 1(2) small teeth composed of 1–2(3) cells; bracteoles like the bracts.

Seta with 8 rows of outer cells surrounding an inner core of 10–22 rows of much smaller cells. Capsule wall 2–3-stratose; outer layer of cells with imperfect two-phase development, the often subquadrate to quadrate primary cells with hyaline walls, usually divided once vertically and once transversely, the secondary walls with strong, sinuous-nodular thickenings; inner layer of cells with numerous semiannular bands.

Spores 10–12 μm in diam., delicately vermiculate-areolate. Elaters straight, 12–13 μm wide.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (ca. 5 m), South Island (20–870 m). Known from Fiordland (Supper Cove, Wilmot Pass), Westland (Omoeroa Saddle), Canterbury (Temple Basin, upper Bealey Valley) and Western Nelson (Dolomite Point) EPs.

Mainly a bog plant. Known from only a few stations. On Stewart Island (track to Mason Bay, ca. 5 m) the species was rather common in standing, stagnant, still water in a *Gleichenia dicarpa* bog with *Leptospermum scoparium – Dracophyllum* shrubs to 1–1.5 m, the margins of water channel typically with a dense cover of *Gleichenia* and *Empodisma minus* and occasional populations of *Dicranoloma*. At this site the species often formed floating mats of various sizes, including one population that measured 40 × 30 cm. Type plants occurred in partial shade of *Halocarpus bidwillii* in a *Sphagnum – Empodisma minus – Halocarpus bidwillii* bog. At Arthur's Pass, it grows in a *Halocarpus bidwillii*, *Chionochloa rubra*, *Carpha alpina*, *Lepidothamnus laxifolius*, *Sphagnum cristatum* tussockland bog, growing through *Sphagnum cristatum*. A specimen from the Wilmot Pass track was collected as a tree-fern epiphyte and a specimen from Dolomite Point, Punakaiki, was in a rock crevice under forest, suggesting that the species occupies a wider habitat.

Comments: This species is easily distinguished by the strikingly asymmetrically bifid leaves, with large, many-celled ventral lobes and reduced, few-celled dorsal lobes. The succubously inserted leaves are inserted to the stem midline dorsally and therefore a broad, leaf-free strip is lacking. The leaves are widely separated on the axis, with up to 7 cortical cells between leaves on each side of the stem. The species may be distinguished from all members of subg. *Zoopsis* by the lack of differentiated papillae of the leaf lobe tips. The underleaves in *Z. macrophylla* are well developed, with discrete lobes. The species has the best-developed central strand of any *Zoopsis*, with the numerous medullary cells collectively much greater in diameter than that of the largest cortical cell. Well-developed plants are freely and laxly pinnate. *Frullania*-type branches are developed from both sides of the main axis and the distinctive lanceolate, many-celled half-leaf is positioned in the angle between branch and stem.

Zoopsis leitgebiana (Carrington & Pearson) Bastow

[Plate 9A; Fig. 108: 4, oil-bodies, p. 469]

Cephalozia leitgebiana Carrington & Pearson, Pap. & Proc. Roy. Soc. Tasmania 1887: 3. *pl. 38*. 1888 (Mar.). *Zoopsis leitgebiana* (Carrington & Pearson) Bastow, Pap. & Proc. Roy. Soc. Tasmania 1887: 269. 1888 (Mar.). Type: New Zealand, *Buchanan*; Tasmania, Mt. Wellington, St. Crispin's Well, *Bastow*; Australia, New South Wales, Balls-head Bay, Sydney, *Whitelegge*.

Zoopsis tenuicaulis Colenso, Trans. & Proc. New Zealand Inst. 20: 253. (May) 1888 (1887). Type: New Zealand, North Is., East Taupo Co., base of Tongariro Mtn. Ra., 1887, *Hill*.

Plants delicate, very soft textured, fleshy but lax, creeping, light green, rather small, to 600(635) μm wide. Branching free, remotely pinnate, the main axis tending to maintain its dominance, the branches of predominantly *Frullania* type; half-leaf normally consisting of a uniseriate row of 2–4 inflated cells, the basal cell notably turgid and up to 2.5× width of the next cell, the base rarely with 2 lateral juxtaposed swollen cells, and in such cases subtend a uniseriate row; ventral-intercalary vegetative branches sparing, leafy as well as geotropic and stoloniform; apices of shoots at times becoming microphyllous, whitish and flagelliform (these sometimes again becoming normal leafy shoots). Axes pellucid and soft textured, in cross section subterete to ellipsoidal, in 6 rows: formed of 4 large cortical cell rows (= lateral merophytes), the dorsal 2 rows larger, + 2 rows of smaller cells (= ventral merophytes); dorsal cortical cells in surface view usually quadrate to 5–6-angled and subisodiametric, leptodermous; medulla of ca. 12–16 rows of much smaller cells, only 13–18 μm in diam. Leaves remote to subcontiguous, normally 1.5–3(4) cortical cells intervening between successive leaves on each side of axis; leaves laterally patent to sometimes dorsally assurgent, succubously inserted, the insertion lines not extending to stem midline dorsally and defining a leaf-free strip nearly 2 cells broad. Leaves relatively small, strongly asymmetric, to 180–220 μm wide × 240–300 μm long to apex of ventral lobe, the lobes persistent; ventral lobe (4)5–8-celled (on weak shoots only 3-celled), at base formed by 2 cells, side-by-side, the lobe proper of (2)3 progressively smaller, inflated, submoniliform cells, infrequently the ventral lobe formed of 2 tiers, each of 2 cells, plus 2 single terminal cells (then 6–7-celled); dorsal lobe reduced, formed of only (2)3 progressively smaller cells; disc 3(4–5) cells wide and 1 cell high, 2 cells wide in suboptimal phases. Leaf cells lax, leptodermous, inflated, those in lobes moniliform and progressively smaller, the end cells usually minute; basal cells and cells of lobe bases 90–120 μm wide × 110–130 μm long. Oil-bodies occupying a small fraction of the cell, dull, opaque, grey, (4)5–8 per basal cell of leaf and ones above, 7–8 per cortical cell, finely and densely papillose, globose to broadly elliptic to fusiform (many short- to long-fusiform), 7 × 9 μm to 7–8.5 × 12–16 μm. Underleaves normally separated by 2–3 tiers of ventral cortical cells, vestigial: normally formed of 2 inflated, sausage-shaped cells, each 30–40 × 55–65 μm, inserted on a "disc" formed of (2)3 quadrate cells, the disc cells usually becoming subdivided, forming a cushion of 8–16 cells from which rhizoids arise; lobe cells each terminated by a small, ephemeral slime papilla. Asexual reproduction normally absent, rarely by tubers.

Dioecious. Androecia spicate, bracts in 3–5 pairs, concave, bilobed, the dorsal lobe subequal to the ventral; antheridia 1 per bract, the stalk uniseriate. Gynoecia on weak, abbreviated ventral-intercalary branches; bracts of innermost series bifid to 0.6 or sometimes 3-fid, the lobes 2(3) cells broad, sublinear, ending in a single cell or a uniseriate row of 2 cells, the margins entire or with a tooth; bracteoles similar but smaller.

Seta with 8 rows of outer cells surrounding an inner core of 10–21 rows of small cells. Capsule wall 2–3-stratose; outer layer of cells mostly subquadrate to quadrate, with imperfect two-phase development, primary cells with hyaline walls devoid of thickenings, usually divided once transversely and once vertically, the secondary walls (both longitudinal and transverse) with strong, sinuous-nodular thickenings; inner layer of cells narrowly oblong, with numerous complete semiannular bands.

Spores delicately areolate. Elaters essentially straight, bispiral to tips.

Distribution and Ecology: New Zealand: Campbell Island, Stewart Island (5 m), South Island (60–1370 m), North Island (10–1200 m), Chatham Islands; Australia: Tasmania, South Australia, Victoria, New South Wales (Meagher and Fuhrer, 2003). An abundant species throughout temperate Australasia. In New Zealand known from Southland, Otago (Dunedin), Westland, Canterbury (Porters Pass), Western Nelson, Southern North Island (Tararua Ra.), Volcanic Plateau, Taranaki, Auckland and Northland EPs.

In New Zealand ranging from Stewart Island to the northern sector of Northland (Radar Bush, WSW of Cape Reinga). Plants are frequent in deeply shaded sites, often in sheltered, humid pockets or recesses, at times occurring deep within such niches. Rather common on steep, often vertical, banks that are often associated with streams or creeks and mostly on damp clayey soils or, less often, on rock, often where sheltered by *Asplenium bulbiferum*, *Blechnum chambersii*, *B. colensoi* and *Leptopteris superba*. Also in hollows formed by exposed tree roots and in protected niches on shaded, vertical cliff faces. Also on saturated, rich, peaty soil of narrow, shallow and stagnant pools in a mixed podocarp–broadleaf forest (South Island, Lake Kaniere Scenic Reserve). This species is often associated with *Lembidium nutans*, which is also a pioneer on mineral soils. Other associated species are *Balantiopsis diplophylla*, *Breutelia pendula*, *Categonium nitens*, *Chiloscyphus spiniferus*, *Distichophyllum pulchellum*, *Fissidens asplenioides*, *F. leptocladus*, *Hypnodendron arcuatum*, *Kurzia hippuroides*, *Leptophyllopsis laxus*, *Philonotis tenuis*, *Pyrrhobryum mnioides* and *Zoopsis argentea*. It also occasionally occurs under *Chionochloa* tussocks in the penalpine and alpine zones, thus overlapping in habitat with *Z. macrophylla*.

Comments: In contrast to *Zoopsis macrophylla*, *Z. leitgebiana* is a relatively weak and slender plant. The leaves are strongly asymmetric as in *Z. macrophylla*, but in *Z. leitgebiana* the larger ventral lobe is usually formed of only 3–4 cells and the dorsal lobe of only 2–3 cells. Leaves in *Z. leitgebiana* on each side are separated by 1.5–3 (less often in part 4) cortical cells vs. up to 7 cells between leaves in *Z. macrophylla*. The underleaves are much smaller than in *Z. macrophylla* and are similar to species of subg. *Zoopsis*: vestigial, formed of 2–3 small, quadrate basal cells and 2 inflated, sausage-shaped cells constituting the 2 lobes, each terminated by a slime papilla. As shoot maturity is approached, the disc cells undergo secondary division and a small transverse "cushion" of up to 8–16 cells is formed; rhizoids originate from such "cushion" cells. Ventral merophytes typically are formed of only 2 tiers of cells, i.e., the underleaves are separated by only 4 cells vs. 7–8 cell tiers (thus 14–16 cells) that separate successive underleaves in *Z. macrophylla*. The stem consists of only 6 rows of cortical cells, the 2 that each belong to lateral merophytes are notably large and inflated, the 2 belonging to the ventral merophytes are much smaller. Medullary cells are minute and, in contrast to *Z. macrophylla*, the entire central strand is narrower in diameter than the largest dorsal cortical cell. Branching, as in *Z. macrophylla*, is commonly of the *Frullania* type, but in this species the half-leaf is typically formed of only 3 cells. The orientation of the half-leaf is also different from *Z. macrophylla*: it lies along the basiscopic side of the branch.

The leaf insertion is more variable than Schuster (1999a) would admit. The insertion lines of the succubously inserted leaves do not extend to the stem midline dorsally, and they delimit a leaf-free strip of, for the most part, 2 cells wide. The leaves often are articulated or inserted directly on the radial walls of the dorsal cortical cells (see Schuster, 1999a, fig. 2: 1, 8, 9) and the leaf-free strip is 2 full cells wide. Such populations often have a leaf disc 3 cells wide. However, in some populations the dorsal extremity of the leaf is inserted on the exposed dorsal-lateral face of the dorsal-most cortical cell and ca. 0.5 of the dorsal-most cortical cell is

leaf-free on each side. This condition approaches that of *Zoopsis macrophylla* (compare Schuster 1999a, fig. 3: 9, 10 with fig. 1: 10).

Tubers were observed in *Engel 20985* from Omahuta Forest Kauri Sanctuary in Northland. These are similar in appearance to the tubers found in *Telaranea tasmanica* (Engel and Merrill, 2004, fig. 32: 1, 2) and represent the first report of this form of asexual reproduction in the genus.

Zoopsis ceratophylla (Spruce) Hamlin

Cephalozia ceratophylla Spruce, Cephalozia 32. 1882. *Paracromastigum ceratophyllum* (Spruce) R.M.Schust., J. Hattori Bot. Lab. 26: 276. 1963. *Zoopsidella ceratophylla* (Spruce) R.M.Schust., Taxon 18: 57, 87. 1969. *Zoopsis ceratophylla* (Spruce) R.M.Schust., Nova Hedwigia 10: 36. 1965, *nom. inval.*, *bas. non cit. Zoopsis ceratophylla* (Spruce) Hamlin, Rec. Domin. Mus., Wellington 7: 311. 1972. Type: Auckland Is., "supra *Chiloscyphum notophyllum* Taylor," *Hooker*.

Cephalozia fissifolia Steph., Sp. Hepat. 3: 314. 1908, *syn. fide* Schuster (1999a). *Paracromastigum fissifolium* (Steph.) R.M.Schust., J. Hattori Bot. Lab. 26: 276. 1963. Type: Auckland Is., *Hooker*.

Plants creeping, light to whitish green, pellucid, nitid when dry, large for the genus, leafy shoots to 1.4 mm wide. Branching common, irregular, the branches of *Frullania* type; ventral-intercalary branches frequent, leafy or stoloniform. Axis subterete, the cortex of 6 rows of cells, the dorsal-most 2 rows of very large, inflated cells, the 2 rows of ventral-lateral cells slightly smaller, the ventral 2 cell rows somewhat but not greatly reduced in size; medulla with 11–15 rows of much smaller, weakly firm-walled cells. Rhizoids few, at underleaf bases only. Leaves strongly succubously inserted, remote to contiguous, widely spreading, plane or essentially so, 270–320 μm wide × 420–550(620) μm long, narrowly oblong to obovate-cuneate, widest in distal half (when not subparallel), nearly symmetrically bilobed to 0.35–0.5; lobes often somewhat spreading, 2–3(4) cells wide at base, formed of (3)5–8 to 10–12 cells, terminating in a uniseriate row of (2)3–5(7) progressively smaller, moniliform cells, the terminal cell sometimes an unspecialized slime papilla; disc 4–5 cells wide at base, the disc rarely with subdivision of cells distally and then to 6–8(10) cells wide, the disc 4–5 cells high (leaf base to sinus base). Cells of leaf disc very large, hyaline, leptodermous, quadrate to hexagonal, (42)45–65(72) × 60–95(115) μm; surface smooth. Oil-bodies (Schuster, 1999a) 10–12 per cell, brownish grey, opaque, finely granular, ellipsoidal to fusiform, 5.5–7 × 11 μm to 6–7 × 16–18 μm. Underleaves relatively large, the 2 lobes each 2–4-celled, terminating in a slime papilla, the disc comprised of 1–2 tiers of 4 cells each. Asexual reproduction by fragmenting or caducous leaf lobes. Fungal partner an ascomycete.

Dioecious. Androecia not seen. Gynoecia on very short, ventral-intercalary branches; bracts and bracteoles much smaller-celled than leaves, bifid to ca. 0.5 or a little less, the lobes terminating in 3–4 strongly elongated cells; disc margins each usually with a few 1-celled teeth and at times a ciliiform process consisting of a uniseriate row of up to 4 strongly elongated cells. Perianth fusiform, cylindrical below, trigonous in distal sector, narrowing toward the mouth, the mouth deeply 6-lobed, the lobes caudate, terminating in 2–3 laterally juxtaposed, distinctly elongated cells that subtend a long, contorted cilium comprised of 4–6 markedly elongated cells (to 8.5:1), the lobes crenulate below the level of the cilium by projecting distal ends of cells, otherwise entire.

Seta with 8 epidermal cell rows and many, much smaller internal cells (Scott, 1969). Capsule not seen.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands, Stewart Island (5–40 m), South Island (35–630 m), North Island (340–940 m). Known from Fiordland (Lake Manapouri), Western Nelson (near Westport) and Southern North Island (Akatarawa Saddle, Tararua Ra.) EPs.

A plant of shaded sites on organic substrates or peaty soil. It occurs over the peaty soil that lines deep hollows at the bases of stumps or dead trees. Also over soil deep in protected niches on the forest floor, at times with a root mass overhang. Also on the sides of bryophyte-covered logs and on tree ferns. On the ridge above Te Kuha, east of Westport, it occurs under *Lepidothamnus intermedius* forest, associated with *Acrobolbus lophocoleoides*, *Acromastigum anisostomum*, *Bazzania adnexa*, *B. hochstetteri*, *Kurzia hippuroides*, *Lepidozia spinosissima*, *Paraschistochila pinnatifolia*, *Rhizogonium pennatum* and *Saccogynidium decurvum*. On Stewart Island (Freshwater Landing, 5 m), in an open area of swamp growing among leaf litter, it was associated with *Telaranea quinquespina* below dense *Gleichenia* ground cover in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium* – *Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus*.

Comments: *Zoopsis ceratophylla* is superficially rather similar to *Zoopsidella caledonica*, both having well-formed, widely spreading, contiguous, symmetrically bilobed leaves with very large cells. *Zoopsis ceratophylla* may be distinguished by the longer, acuminate leaf lobes with strongly moniliform cells and the caducous leaf apices vs. the always persistent leaf lobes, which are few-celled, triangular and terminate nearly uniformly in 2 cells in *Z. caledonica*. Cytological distinctions between the two species are distinctive and useful, particularly when the two species grow together. Oil-bodies are opaque, brownish grey and finely granular in *Z. ceratophylla* vs. glistening, hyaline, smooth and homogeneous or nearly so in *Z. caledonica*. Seta anatomy differs strikingly between the two plants: 8 rows of outer cell rows and many, much smaller internal cells (Scott, 1969) vs. 8 outer rows and 4 rows of similar-sized internal cells in *Z. caledonica*. *Zoopsis ceratophylla* is much less common than *Z. caledonica*.

Zoopsis matawaia M.A.M.Renner

[Plate 9I; Fig. 110: 1, oil-bodies, p. 486]

Zoopsis matawaia M.A.M.Renner *in* M.A.M.Renner, E.A.Brown and Glenny, J. Bryol. 28: 334. *f. 2*. 2006. Holotype: New Zealand, South Is., Westland ED, Omoto State Forest, Kaiata Ra., Rata Tree Peak, 290 m elevation, *Renner and Paul CMSAX118* bryoplot 1 (CHR 564879!); isotype: (F!).

Plants soft textured, procumbent, nitid, the shoots (600)860–1050 μm wide and at least 25 mm long. Branching copious, lateral branches exclusively *Frullania* type, pseudo-dichotomous, predominantly from one side of the axis; ventral-intercalary branches present, giving rise to leafy shoots, rarely to microphyllous axes. Axes subterete, the cortical cells in 6 rows, inflated, the dorsal cortical cells uniformly leptodermous, 110–140 μm wide, 90–180 μm long, the 2 ventral rows consistently the smallest (= ventral merophyte); medullary cells in 7–9 rows, narrow, forming a discernible central strand (clearly visible in dorsal view of the shoot). Rhizoids present, hyaline, smooth, produced from a small distinct rhizoid initial field at the base of the underleaves, not produced at leaf bases, the tips bulbous. Leaves remote, with 1 cortical cell intervening between successive leaves on each side of axis; leaves widely spreading,

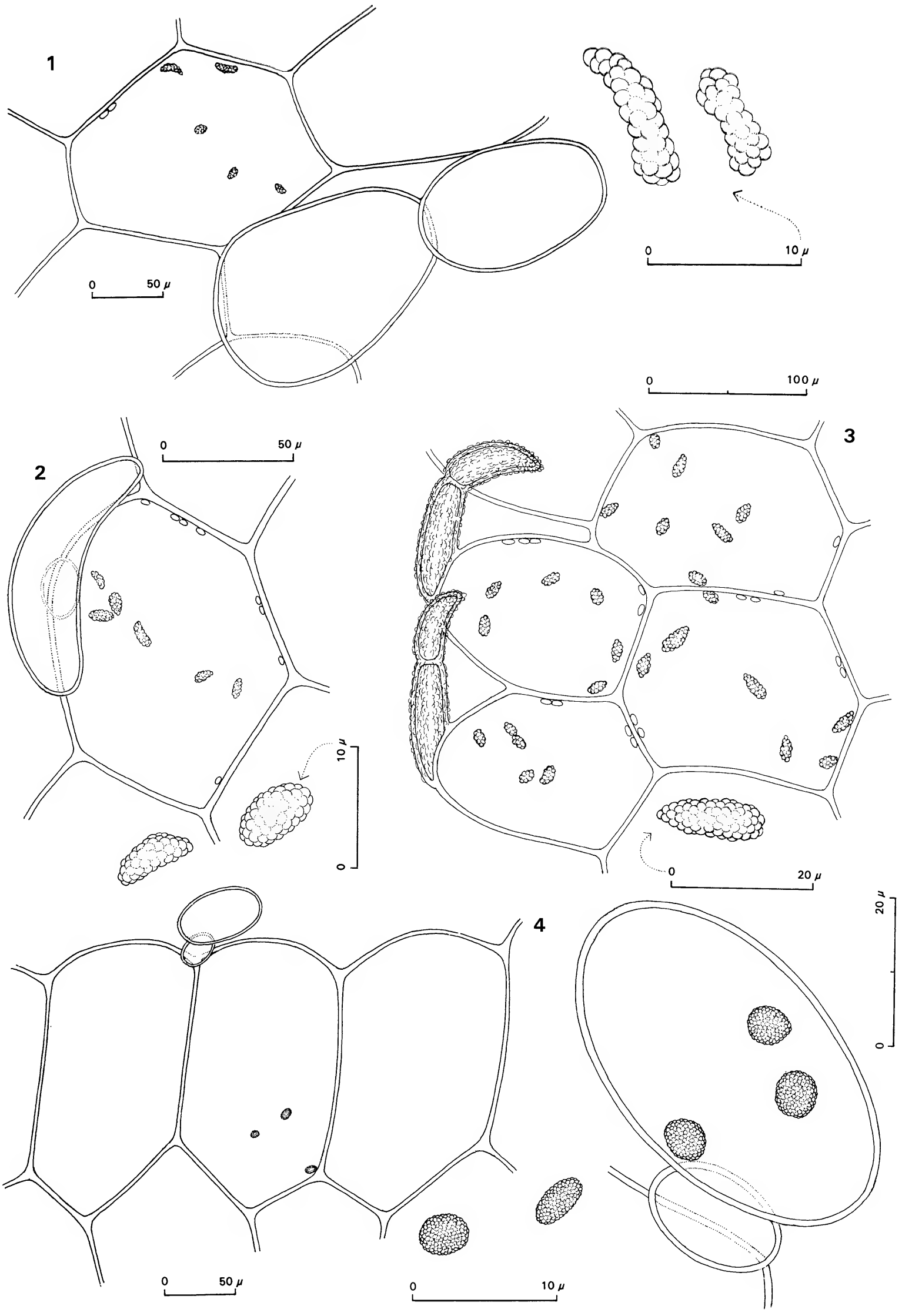

Fig. 110.
Oil-bodies. 1. *Zoopsis matawaia* M.A.M.Renner. Stem cell with oil-bodies, at right 2 oil-bodies at higher magnification (+ leaf lobe). 2. *Zoopsis argentea* var. *flagelliformis* (Colenso) R.M.Schust.

equally bilobed, the postical lobe lying slightly over the antical in dorsal view; the 2 basal cells fused for ca. two thirds their length, similar in size to the dorsal cortical cells of the stem, being 105–130 μm wide × 115–175 μm long; lobes (on leaves in mature shoot sectors) consisting of a uniseriate row of 2–3 large, inflated, thin-walled, moniliform cells that are constricted at septa, the lobes readily fragmenting; lobes of embryonic leaves (visible in this state only at the shoot apex) initially with up 7–8 uniseriate rows of cells, the terminal cell not capped by a crescent-shaped hyaline papilla. Cells of leaf serially decreasing in dimensions toward the apex, the next cell 80–100 μm wide × 115–135 μm long, the third (usually apical) cell 45–55 μm wide × 70–90 μm long. Oil-bodies in cells of stem and leaf, occupying tiny fraction of and inconspicuous portion of cell lumen, scattered irregularly throughout the cell lumen, hyaline and glistening, (0)4–6(8) per cell, moderately botryoidal but (with age) becoming conspicuously botryoidal when spherules coalesce and then oil-bodies irregularly bulging, the oil-bodies rather irregular in shape, often ellipsoidal, narrowly linear, often crescentic, 2–4 × 6–9 μm. Underleaves separated by 2 pairs of ventral merophyte cells, except at *Frullania*-type branches, where underleaves are separated by 3 pairs of cells, bifid nearly to base, consisting of 2 basal, subisodiametric cells (often longitudinal division of 1 or both cells results in a "disc" of 3–4 laterally juxtaposed cells); lobes divergent, initially in a uniseriate row of 3–4 cells or more cells, but, like leaves, soon fragmenting and typically leaving only the 2 basal cells, though these may also be absent on mature stem sectors, the basal cells 60–70 μm wide × 90–100 μm long, typically united for 0.15 their length. Underleaves rarely to occasionally composed of 2 subisodiametric basal cells + only 2 single-celled lobes, each capped by a single obpyriform hyaline papilla. Asexual reproduction by single-celled fragments derived from the leaf lobes.

Androecia and gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (290–750 m). Known from the Westland and Western Nelson EPs between mountains east of Lake Kaniere (Mt. Brown) and the southern end of the Paparoa Ra. (Mt. Ryall) and as far east as the Haupiri River valley (Mt. Mason). Found in forests on hillslopes of *Dacrydium cupressinum*, *Metrosideros umbellata*, *Weinmannia racemosa* and *Quintinia serrata*, on inclined humic soil on the floor of tree-root caves, mostly under *Metrosideros umbellata*, but also known from a tree-root cave under *Pseudowintera colorata* and from an overhanging surface of a rotting log. The sites are characterized by low light conditions and protection from direct rainfall, and the species can form extensive pure mats. Accompanying species are *Leucobryum candidum*, the creeping vine *Metrosideros diffusa*, *Psiloclada clandestina*, *Saccogynidium australe*, *Zoopsis argentea* and *Z. bicruris*.

Comments: *Zoopsis matawaia* is characterized by its lack of a multicellular disc, the leaves being divided nearly to their base into 2 uniseriate lobes, with the basal pair of cells partially

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Thallus cell with oil-bodies, below 2 oil-bodies at higher magnification. 3. *Zoopsis setulosa* Leitg. Thallus cells with oil-bodies, at lower right an oil-body at higher magnification. 4. *Zoopsis bicruris* Glenny & E.A.Brown. At left 3 cortical cells with a leaf, below right 2 oil-bodies at higher magnification; at right a leaf cell with 3 oil-bodies. (Fig. 1, from *Glenny 9097*, New Zealand, South Is., Westland EP, Mt. Brown; 2, from *Glenny 9236*, New Zealand, South Is., Western Nelson EP, Takaka Hill, Harwoods Hole Track; 3, from *Glenny 8877*, New Zealand, South Is., Westland EP, Mt. Te Kinga, Lake Swan; 4, from *Glenny 9098*, New Zealand, South Is., Westland EP, Mt. Brown.)

united. The leaves and underleaves fragment, a feature shared with *Z. ceratophylla* and *Zoopsidella caledonica*.

Zoopsis matawaia most resembles *Z. leitgebiana* in having patent, few-celled, succubously inserted leaves composed of a few large cells of approximately the same dimensions as the dorsal cortical cells. Also, the underleaves on mature sectors of the shoot are composed of only 2 cells that are separated nearly or completely to the base. *Zoopsis matawaia* is distinguished from *Z. leitgebiana* by its readily fragmenting leaf lobes, its symmetrically bilobed leaves, its leaves being consistently separated by one cortical stem cell, as opposed to 1–3 cortical cells and its pseudo-dichotomous, as opposed to irregularly pinnate, branching. In *Z. matawaia* the leaves do not consistently extend onto the dorsal stem surface, usually leaving the two rows of cortical cells entirely leaf-free.

Zoopsis argentea (Hook.f. & Taylor) Gottsche, Lindenb. & Nees

[Plate 9B, E; Fig. 110: 2, oil-bodies, p. 486]

Plants ribbon-like, loosely creeping, pale green to pure green in dense shade, to 440 μm wide with rudimentary leaves (to 825 μm wide in var. *flagelliformis*). Branching common, pseudo-dichotomous, the branches of *Frullania* type, more vigorous and displacing the parent axis to one side, the branches often from only one side of axis; ventral-intercalary branches forming normal axes with rudimentary leaves, or hyaline, geotropic flagelliform axes, the geotropic axes with leaves reduced to solitary papilliform cells; apices of shoots at times becoming microphyllous and flagelliform. Axis dorsiventrally flattened, biconvex to less often planoconvex, formed of 2(3) rows of exceedingly large, polygonal to hexagonal cells (4–5 cells broad in var. *flagelliformis*), the lateral projections being rudimentary leaves; axis in ventral aspect with 6 cell rows, the 2 median rows (the ventral merophyte) somewhat narrower compared to the cells of the lateral merophytes (the ventral sectors of the lateral merophytes each 3–4 cells wide in var. *flagelliformis*); medulla composed of ca. 10–12 very narrow, strongly elongated cells, forming a small central strand. Rhizoids in fascicles from bases of the vestigial underleaves, the rhizoids with swollen, contorted and/or dendritic tips, the rhizoids forming a conspicuous haustorial disc in var. *flagelliformis*. Leaves reduced, separated by intervals formed by more than a full cortical cell, consisting of 2-celled, crescentic, lateral projections, each cell inflated and bearing at its apex a crescentic, hyaline, smooth papilla that is connate to the lobe cell along the outer bulge (the papilla on the proximal cell usually slightly larger, 85–90 μm long vs. 45–55 μm long for the papilla on the anterior cell), the leaves consisting of 3–4 cells in var. *flagelliformis*. Oil-bodies occupying tiny fraction of cell, very pale and somewhat grey, (6)8–9(11) per upper thallus cell, subglobose to elliptic to fusiform, coarsely papillose, 3.8–4.3 × 6.2–7.2 μm to 3.4–4.3 × 8.2–9.6 μm. Underleaves vestigial, consisting of 2, small, contiguous, inflated cells, each bearing an elongated, hyaline cell, which may bear a small, terminal hyaline papilla. Asexual reproduction absent. Fungal partner an ascomycete.

Androecia on ventral-intercalary branches; bracts leaf-like, bilobed, concave; antheridia 1 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches from normal, ribbon-like shoots, or lateral- or ventral-intercalary from geotropic, flagelliform axes; bracts and bracteoles similar, those of innermost series bifid to 0.5–0.65(0.75), the lobes often narrow, terminating in a single cell or a uniseriate row of 2–4(6) cells, the margins often with

a small lateral tooth. Perianth fusiform to obpyriform-fusiform, unistratose, the mouth deeply 6-lobed, the lobes narrow, (2)3–4 cells broad at base and with a few to several biseriate tiers, terminating in a uniseriate row of 5–6 moniliform cells.

Seta with 8(9) rows of outer cells surrounding an inner core of 10–16(19) rows of much smaller cells. Capsule broadly ellipsoidal, the wall 2-stratose; outer layer of cells with primary walls hyaline, each with 1 longitudinal secondary wall and sporadically a transverse wall, the secondary walls with brown nodular thickenings that are confluent, the walls appearing sinuous; inner layer of cells with weak, yellowish brown semiannular bands.

Spores 13–17 μm in diam., pale brown, delicately areolate. Elaters 8.5–10 μm wide, bispiral, the spirals 2.4–2.6 μm wide.

Comments: An extraordinary plant. The leaves are comprised of 2 projecting chlorophyllose basal cells, each at its summit with a sausage-shaped or crescentic, smooth, 1-celled papilla that is attached by its longer side. *Zoopsis setulosa* also has leaves formed by 2 projecting chlorophyllose basal cells, but in that species each of the 2 basal cells has a 2-celled appendix that is falcate or hooked and has a conspicuously roughened surface. Also, the appendix is attached by the narrow base of the basal cell.

Zoopsis argentea may be subdivided into two varieties, as follows.

Key to Varieties

1a. Plants to 455 μm wide, the axis and rudimentary leaves moderately flattened, not band-shaped; axis proper formed dorsally of 2 rows of cells (with at most sporadically a cell once-septate); ventral face of plant of 4 cell rows (leaves included); ventral side of axis and ventral leaf bases lacking conspicuous rhizoid-initial discs
. . . . . var. *argentea* (p. 489)

1b. Plants to 825 μm wide, axis and rudimentary leaves strikingly flattened, forming a band-like thallus; axis proper, at maturity, formed dorsally of 4–5 rows of cells; ventral face of plant of up to 8–10 rows of cells; ventral side of axis with conspicuous rhizoid-initial discs at bases of rudimentary underleaves, and locally at leaf bases
. . . . . var. *flagelliformis* (p. 490)

Zoopsis argentea (Hook.f. & Taylor) Gottsche, Lindenb. & Nees var. ***argentea***

Jungermannia argentea Hook.f. & Taylor, London J. Bot. 3: 400. 1844. *Zoopsis argentea* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 473. 1846. *Cephalozia argentea* (Hook.f. & Taylor) Lindb., J. Linn. Soc., Bot. 13: 191. 1872. Type: Auckland Is.

Plants to 455 μm wide, axis and rudimentary leaves moderately flattened, not band-shaped; axis proper formed dorsally of 2 rows of cells (with at most sporadically a cell once-septate); ventral face of axis of 4 cell rows (leaves included); ventral side of axis lacking conspicuous rhizoid-initial discs.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, Stewart Island (30–220 m), South Island (0–960 m), North Island (25–920 m), Chatham Islands; Australia: Tasmania, Western Australia, Victoria, Australian Capital Territory, New South Wales (Meagher and

Fuhrer, 2003). In New Zealand known from Fiordland, Southland, Otago, Westland, Western Nelson, Marlborough, Southern North Island, Gisborne, Volcanic Plateau and Northland EPs.

A plant of moderately to well-shaded sites and often on organic substrates. It is rather common on rotted, decorticated, often bryophyte-covered logs or stumps (at times where the wood is crumbly) and particularly on the sides, or lower halves of the sides, where moister conditions prevail. Also rather common on the bases and trunks of tree ferns, particularly of *Dicksonia squarrosa*, both of living individuals as well as those that are old, rotted, moist and prostrate. Also on dead stipes of the tree fern *Cyathea dealbata*, being one of few plants invading that surface. Also at tree bases or among exposed roots, especially the meshing of roots, particularly where some soil has accumulated, and plants at times are present in the niche notable for the genus *Zoopsis*: deep in shaded, protected recesses or hollows at tree bases or tree buttresses. Less often over bare soil of protected, moist pockets or hollows of banks or slopes. Recorded as an epiphyte on tree trunks of *Weinmannia racemosa*, *Dacrydium cupressinum*, *Libocedrus bidwillii* and *Dracophyllum arboreum*. Exceptionally in protected niches of large rock outcrops. Associated with *Bazzania adnexa*, *B. nitida*, *Canalohypopterygium tamariscinum*, *Chiloscyphus echinellus*, *Cyathophorum bulbosum*, *Distichophyllum pulchellum*, *Kurzia hippuroides*, *Leptotheca gaudichaudii*, *Leucobryum candidum*, *Orthorrhynchium elegans*, *Psiloclada clandestina*, *Rhizogonium distichum*, *R. pennatum* and *Telaranea herzogii*.

Comments: In the var. *argentea* the axis is formed dorsally of 2 cell rows, or at times 3 cell rows, through subdivision of one of the two dorsal cortical cells. The cortex consists normally of 8 cells. Cross sections usually reveal 2 inflated, exceptionally large dorsal cortical cells, flanked on either side by a cell (the chlorophyllous, basal leaf cell). On the ventral side, the cortex is normally formed of 6 cells, the two smaller median ones representing the ventral merophyte, the two on each side constituting the lateral merophytes.

Zoopsis argentea var. ***flagelliformis*** (Colenso) R.M.Schust.

[Fig. 110: 2, oil-bodies, p. 486]

Zoopsis flagelliformis Colenso, Trans. & Proc. New Zealand Inst. 18: 250. 1886, "*flagelliforme*."
Zoopsis argentea var. *flagelliformis* (Colenso) R.M.Schust., Nova Hedwigia 68: 38. 1999. Type: New Zealand, North Is., Waipawa Co., Norsewood, 1885, *Colenso*.
Zoopsis basilaris Colenso, Trans. & Proc. New Zealand Inst. 21: 77. 1889 (1888). Type: New Zealand, North Is., Waipawa Co., S of Dannevirke, 1888, *Colenso 1301*.
Zoopsis muscosa Colenso, Trans. & Proc. New Zealand Inst. 21: 78. 1889 (1888). Type: New Zealand, North Is., Waipawa Co., near Dannevirke, 1888, *Colenso*.

Plants to 825 μm wide, axis and rudimentary leaves strikingly flattened, forming a band-like thallus; axis proper, at maturity, formed dorsally of 4–5 rows of cells; ventral face of plant of up to 8–10 rows of cells; ventral side of axis with conspicuous rhizoid-initial discs at bases of rudimentary underleaves, and locally at leaf bases.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (sea level), South Island (110–800 m), North Island (sea level). Known from Rakiura (Port Pegasus), Otago (Table Hill), Westland (Fox Glacier), Western Nelson (Moa Park), Southern North Island (Norsewood, Dannevirke) and Gisborne (Urewera Natl. Park) EPs. At Moa Park (N Arthur Ra., 760 m) it occurred under *Nothofagus fusca* forest on damp humus and was growing with *Chiloscyphus echinellus*, *Kurzia hippuroides*, *Telaranea gibbsiana* and *Zoopsis setulosa*.

Comments: This taxon exhibits an extreme expression of shoot elaboration within the genus, showing the closest approach to a thallus, with the leaf rudiments poorly set off from the "frond." The var. *flagelliformis* typically has a much more elaborate, more frond-like structure than that of the typical variety. One or both of the 2 chlorophyllous leaf cells may be subdivided, so that the leaf is often formed of 3–4 chlorophyllous cells. In addition, the dorsal cortical cells are secondarily divided, so that the axis becomes 4–5 cell rows broad, rather than the 2 rows usually found in var. *argentea*. In ventral aspect, the ventral merophyte remains 2 cells broad, but the ventral portions of the two lateral merophytes become 3–4 cells broad, resulting in a "frond" that (leaves included) is 11–12 cells across. Such fronds may bear conspicuous, fasciculate rhizoids, forming haustorial discs, produced from the underleaf bases as well as (often) from the bases of the leaves.

Zoopsis bicruris Glenny & E.A.Brown

[Plate 9C; Fig. 110: 4, oil-bodies, p. 486]

Zoopsis bicruris Glenny & E.A.Brown *in* M.A.M.Renner, E.A.Brown and Glenny, J. Bryol. 28: 332. *f. 1*. 2006. Holotype: New Zealand, Westland, Blackball, Croesus Track, 300 m elevation, *Glenny 8281* (CHR 5361880); isotypes: (NSW, WELT).

Plants creeping, glossy, yellow-green, the shoots to 10 mm long, to 0.45 mm wide at the widest point, widest below the tip, never attenuate, the apex acute. Branching frequent, the branches strictly of ventral-intercalary type; ventral-intercalary flagellae present. Rhizoids absent. Axes broad and flat, plano-convex to biconvex, comprised uniformly of thin-walled cells; dorsal surface comprised of 2 rows of large, inflated cells that form the lateral margin of the axis, the cells 210–250 μm wide × 130–150 μm long; ventral surface comprised of 4 rows of cells, the median 2 rows composed of cells 47–88 wide × 40–70 μm long, the outer 2 rows composed of cells 95–150 μm wide × 53–68 μm long; medullary cells in 9 rows, thin-walled, forming a central strand. Leaves distant, with 2 dorsal cortical cells intervening between successive leaves on each side of axis; leaves transversely oriented, bifid, consisting of 4 cells: the basal pair of cells (the "disc") touching, small and rather inconspicuous, the dorsal "disc" cell on the side of the stem over the wall between 2 dorsal stem cells, the ventral "disc" cell at the junction of 2 dorsal stem cells and 2 ventral stem cells, the basal cells each distally with one large and conspicuous ovoid cell (the "lobes"); basal cells 30–32 μm in diam., packed with oil-bodies; distal cells each 26–41 × 42–88 μm, without oil-bodies and chloroplasts each in turn capped by a slime papillae that eventually collapses and is usually not visible. Oil-bodies in dorsal cortical cells 2–5 per cell, inconspicuous and occupying a tiny fraction of cell lumen, opaque, pale grey, hyaline and glistening, finely papillose, globose to elliptic; in leaf cells 6 per cell, conspicuous but still occupying a small fraction of lumen, coarsely papillose, with spherules larger than those of the cells. Underleaves vestigial, distant, separated by 3 pairs of ventral cortical cells, bifid, consisting of 2–3 basal, subisodiametric cells (the "disc"), each with an inflated, sausage-shaped cell terminating in a slime papilla.

Dioecious. Androecia unknown. Gynoecia on short ventral-intercalary branches; bracts and bracteoles bifid, the terminal cell of lobes internally sparsely papillose to smooth, the cells of bracts mostly hyaline, without oil-bodies. Perianth cylindrical, the apex unlobed but dentate by ca. 13 teeth, each tooth of 1–2 cells.

Seta ca. 1.6 mm long at maturity, with 8 rows of outer cells surrounding inner core of ca. 9 rows of smaller cells. Capsule wall bistratose, 20 μm thick.

Spores 13–14 μm in diam., finely reticulate-ridged. Elaters 9–12 μm wide, bispiral.

Distribution and Ecology: Endemic to New Zealand: South Island (300–960 m), Chatham Islands. In the South Island known from Westland and Western Nelson EPs, the southern limit near Lake Kaniere (Mt. Brown), the northern limit at Stockton Plateau.

Found in forests of *Dacrydium cupressinum*, *Metrosideros umbellata* and *Weinmannia racemosa* and stunted forest or scrub of *Lepidothamnus intermedius*, *Halocarpus biformis*, *Nothofagus solandri* var. *cliffortioides*, *Metrosideros umbellata* and *Lagarostrobos colensoi*. Usually on humus on the floor of root caves under *Metrosideros umbellata*, *Weinmannia racemosa* or *Lepidothamnus intermedius*. Accompanying species in these cave sites are *Acromastigum colensoanum*, *Bazzania nitida*, *Categonium nitens*, *Kurzia hippuroides*, *K. tenax*, *Psiloclada clandestina*, *Rhizogonium distichum*, *R. pennatum*, *Zoopsis argentea*, *Z. ceratophylla*, *Z. leitgebiana*, *Z. matawaia* and *Z. setulosa*. Found on Mt. Augustus (Stockton Plateau, 960 m) on an overhanging wet rock face in a deeply shaded boulder pile under *Nothofagus solandri*, *Halocarpus biformis* and *Metrosideros umbellata* scrub where it was mixed with *Telaranea inaequalis* and *Acromastigum cunninghamii*.

Comments: *Zoopsis bicruris* is similar to *Z. nitida* in having very reduced leaves giving the shoots a worm-like appearance. The species is unique in the genus in its complete lack of terminal branching, the branches being exclusively ventral-intercalary in origin. *Zoopsis bicruris* differs from other *Zoopsis* species with reduced leaves (*Z. nitida*, *Z. argentea* and *Z. setulosa*) in having clavate shoot apices that narrow abruptly to an acute tip. This feature is distinctive in the field. The leaf-disc cells are only ca. 30 μm in diam., much less than the cortical stem cells of ca. 100–200 μm diam., whereas in other species of *Zoopsis* with reduced leaves, the disc cells are equal in size to the cortical stem cells. This gives the stem in those other species the appearance of being 4 cells wide whereas in *Z. bicruris* the stem is clearly only 2 cells wide on the dorsal surface. The leaf lobe cells are inconspicuous and collapse when the shoots become partially desiccated, giving the appearance in the field of a leafless stem 2 cell rows wide.

Zoopsis nitida Glenny, Braggins & R.M.Schust.

[Plate 8C, 9F]

Zoopsis nitida Glenny, Braggins & R.M.Schust., J. Bryol. 19: 776. *f. 1*. 1997. Holotype: New Zealand, North Auckland, Waipoua Forest, Lookout track, 100 m, *Glenny 5474* (WELT); isotype: (CHR).

Plants vermiform, creeping, pure green, highly nitid, to 550 μm wide. Branching sparing, the branches sporadically furcate, of *Frullania* type; ventral-intercalary branches common, frequently stoloniform. Axes flat or somewhat convex dorsally, rounded into the margins, the dorsal cortical cells in 2 rows, the cells prominent, convex, their inner margins forming a zigzag median line; lateral margins of axis on each side comprised of a row of inflated cells considerably smaller than those of the dorsal cortical cells; ventral surface comprised of 2 narrow, elongate cells (= ventral merophytes), these flanked on each side by (1)2(3) rows of larger subisodiametric cells; medulla of 9–12 rows of small, strongly elongated cells forming a well-defined central strand. Rhizoids few, short, at bases of underleaf vestiges and at lateral leaf bases, the apices sometimes dilated and/or incipiently lobed. Leaves rudimentary and ephemeral, visible only at shoot apex, usually a mere thin-walled, spur-like, hyaline solitary

cell inserted laterally on one of the lateral (superficially dorsal) cells (the collapsed remnants of these visible at times on mature axis margins); the "leaf" usually elongate or acuminate and pointed, sometimes turned toward the axis apex, its anterior margin at times with a delicate, soon-collapsed hyaline papilla; leaf rudiments rarely 2–3-celled, then formed of vestigial lobes, each of 1–2 cells. Oil-bodies (Schuster, 1999a) finely granular or granular-botryoidal, smaller and fewer in dorsal cortical cells, ca. (3–4)5–16 per cell; ventral surface of axis with more numerous and larger oil-bodies, the lower lateral cortical cells adjoining the ventral cortical cells with ca. 14–25 oil-bodies per cell; oil-bodies in the elongated ventral cortical cells ca. 15–30, crowded, only marginally smaller than those of adjoining cells. Underleaves rudimentary and ephemeral, near shoot apices consisting of 2 subquadrate to subglobose cells ("disc") from which rhizoids originate and 2 short-cylindrical 1-celled "lobes," the lobe cells each terminating in an ephemeral, minute, hyaline papilla. Asexual reproduction lacking.

Androecia at apices of abbreviated, weak, ventral-intercalary branches; bracts few-celled, bilobed; antheridia 1 per bract, the stalk uniseriate. Gynoecia on feeble, ventral-intercalary branches; bracts oblong-ovate, 3-lobed, but often with a third smaller lobe or tooth; lobes acute, 2–5 cells wide at base, terminating in a uniseriate row of 2–3(4) cells. Perianth urceolate to obpyriform, wide at the mouth, deeply divided into 6 slender lobes, the lobes 2 cells wide near base, terminating in a uniseriate row of 2–3 progressively smaller cells.

Seta with 8 rows of outer cells surrounding an inner core of 12–13 rows of small cells. Capsule not seen.

Spores 15 μm in diam., delicately reticulate, the ridges low. Elaters bispiral, the spirals delicate.

Distribution and Ecology: Endemic to New Zealand: South Island (100–200 m), North Island (240–680 m). Known from Westland (Lake Matheson, Mt. Te Kinga, Bullock Creek) and Northland (Waipoua Forest, Tutamoe Ra.) EPs.

The species occurs in lowland forest among tree roots, in tree root caves on humus, on the lower side of a rotten tree trunk and on the base of the caudex of *Cyathea dealbata*, in humid, usually rather shaded situations (but not in so consistently strongly shaded habitat as *Zoopsis bicruris*). It occurs in various lowland forests: tall podocarp forest mostly comprising *Dacrydium cupressinum* (Lake Matheson, S Westland, 100–200 m), *Weinmannia racemosa – Quintinia serrata – Metrosideros umbellata* forest (Mt. Te Kinga, 400 m), *Agathis australis – Metrosideros robusta* forest with a *Cyathea dealbata* understory (at the type locality) and *Weinmannia silvicola – Melicytus ramiflorus* forest with an understory of *Cyathea smithii*, *Ripogonum scandens* and *Freycinetia baueriana* (Tutamoe Ra., Northland, 480 m). Accompanying species are *Bazzania adnexa*, *Calomnion complanatum*, *Kurzia hippuroides*, *Leucobryum candidum*, *Mittenia plumula*, *Psiloclada clandestina*, *Saccogynidium australe*, *Schistochila appendiculata*, *Sticta filix*, *Telaranea herzogii*, *Zoopsis argentea*, *Z. bicruris*, *Z. ceratophylla* and *Z. setulosa.*

Comments: *Zoopsis nitida* has the most reduced leaves of any species in the genus. The 1-celled rudimentary leaves with a hyaline papillae are present at the shoot apex but collapse as the shoot matures.

The species is most likely to be confused with the rudimentary-leaved *Zoopsis bicruris*. In the field, the two can be separated by the shape of the apex, uniformly tapering in *Z. nitida* whereas *Z. bicruris* has a clavate apex that narrows suddenly to the tip; *Z. nitida* has 4 rows of cells visible on the dorsal stem surface while *Z. bicruris* only has two. Terminal branches will

confirm the presence of *Z. nitida*. Under the dissecting microscope the leaves are difficult to see in both species, but the difference in the number of dorsal stem cell rows easily differentiates them and is the easiest way to identify dried specimens. In Westland the two may be found growing together.

Schuster (1999a, p. 53) remarks that this species is "... one of the most distinctive of all hepatics" and it takes the trend toward the thallose condition further than any other *Zoopsis* species.

Zoopsis setulosa Leitg.

[Plate 9D, G, H; Fig. 110: 3, oil-bodies, p. 486]

Zoopsis setulosa Leitg., Mitth. Naturwiss. Vereins Steiermark 6: 24. 1876. *Cephalozia setulosa* (Leitg.) Spruce, Cephalozia 27. 1882. Type: New Zealand, North Is., "um Auckland," *Novara Expedition*.

Plants ribbon-like, pale green, markedly nitid when dry, to 600 μm wide. Branching common, the branches usually mostly of *Frullania* type; ventral-intercalary branches also common, often geotropic and microphyllous. Axes planoconvex, consisting of 2 rows of dorsal cortical cells, the cells very large, isodiametric or wider than high, their inner margins forming a zigzag median line; ventral cortical cells in 4 rows: 2 lateral rows (= lower cells of lateral merophytes) on each side subequal to the dorsal cortical cells, and 2 rows of cells constituting the ventral merophytes rather broad, the cells smaller than those of the 2 lateral rows, subquadrate; medulla of 19–22 rows of small cells forming a central strand. Leaves distinctly projecting laterally, each typically separated on the same side of axis by less than half of a marginal cortical cell; leaf consisting of two 1-celled, ovoid-conoidal basal cells connate to each other for 0.5–0.65 their length, the apices broadly rounded, each bearing a 2-celled setose appendage; appendages conspicuous, attached by the narrow basal-lateral side of the basal cell, arched to geniculate, the distal cell tapered to the summit, curved over the basal leaf cell, the surface of the appendage cells strongly papillose. Oil-bodies 5–10 per thallus cell, occupying a very small portion of volume of lumen, hyaline, moderately botryoidal, elliptic to linear to fusiform to crescentic, 5.8–7.7 × 17.8–20.6 μm, a few smaller, more broadly elliptic and 5.3–6.2 × 11.5–14.4 μm, a few linear and 4.3 × 17.3 μm. (In a short time the spherules enlarge and the oil-body perimeter becomes irregularly bulged.) Claw-like cells of the leaf lobes thick-walled, with numerous chloroplasts, but with fewer and considerably smaller oil-bodies, only 2.9 × 3.8–5.3 μm. Underleaves separated by 2 tiers of 2 cells each, rudimentary, consisting of 2–4 subspherical basal cells ("disc") and two 1-celled "lobes," the lobe cells each terminating in a hyaline papilla. Asexual reproduction lacking.

Androecia and gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (20–30 m), South Island (130–630 m), North Island ([240]720–890 m); Australia: Tasmania, Victoria, New South Wales (Meagher and Fuhrer, 2003). Known in New Zealand from Fiordland, Westland, Western Nelson, Auckland and Northland (Waipoua) EPs.

Sporadic and scattered sites over a broad range, occurring on Stewart Island, on the South Island in Westland north to the Marino Mtns. in Nelson, and in the North Island in scattered, mostly middle-elevation stations, e.g., at 720–750 m in the Herangi Ra. (S of Kawhia Harbor), 880–890 m on Mt. Te Aroha, 835 m on Table Mtn., 650–680 m on the Hauturu Highpoint

Track and 800 m on Mt. Moehau. The species occurs in shaded, protected, humid niches within forests. It occurs over peaty soil in well-shaded hollows or pockets, a characteristic niche, and in such situations it may cover large areas. Also, in the Herangi Ra. (S of Te Whakapatiki), on soil of a small vertical bank in a very narrow and shallow water channel in a small valley system, with vegetation consisting of *Podocarpus hallii*, *Dracophyllum traversii* and *Weinmannia* to 3–5 m tall. In the Paparoa Ra. (upper slopes of N side of Tiropahi River) over soil under a granitic ledge at 130–170 m in dense scrub dominated by *Nothofagus menziesii* and *N. solandri* with scattered *Dacrydium cupressinum*, *Freycinetia baueriana*, *Dicksonia squarrosa*, *Coprosma* spp. and *Brachyglottis*. On Stewart Island (Fern Gully Track) over humus of the floor in a forest with a canopy of *Fuchsia excorticata* and *Griselinia littoralis*, and an understory of *Blechnum discolor*. Species associated with *Z. setulosa* are *Bazzania adnexa*, *B. nitida*, *Cryptopodium bartramioides*, *Distichophyllum kraussei*, *D. pulchellum*, *Hymenophyton leptopodum*, *Kurzia hippuroides*, *Lepidozia spinosissima*, *Leucobryum candidum*, *Psiloclada clandestina*, *Rhizogonium distichum*, *Thuidium furfurosum* and *Wijkia extenuata*.

Comments: A distinctive species, recognizable at a glance because of the leaves, which are closely contiguous and formed of two large chlorophyllous cells, each free distally, so that the leaf appears bilobed, bearing a hooked, slender, 2-celled "appendix." The precise arrangement of the leaves lends a distinctive, crisp regularity to the plants vs. the somewhat irregularly scalloped margins of shoots of *Zoopsis argentea*. The surface of the incurved appendices is roughened, while the surface of the chlorophyllous cells is smooth. The leaves are closely juxtaposed on each side of the stem and only a fraction of one cortical cell intervenes between leaf bases.

Zoopsidella R.M.Schust.

Zoopsidella R.M.Schust., Nova Hedwigia 10: 24. 1965.

Plants markedly distichous-leaved and strongly complanate, prostrate or creeping, light to pale green, nitid, rather translucent, small, the tips occasionally becoming flagelliform, the plants small to medium, to 1.6 mm wide. Branching sparing and irregular, the branches normally ventral-intercalary, often stoloniform and microphyllous; *Frullania*-type branches sometimes also present (in ours). Stem with 6 or 10–13 rows of large, hyaline cortical cells forming a conspicuous hyaloderm, the dorsal rows of large cells in surface view irregularly polygonal and not or little elongated, the cells of the ventral merophyte smaller than the dorsal and lateral cells; medullary cells markedly smaller, firm-walled. Rhizoids at the bases of underleaves or (extraterritorial species) sometimes also from ventral side of apical and subapical leaf cells, often with bulbous apices. Leaves typically formed of many cells, laterally spreading, nearly or quite flat, almost longitudinally inserted, leaving a broad strip of 2–3(5) cell rows leaf-free; leaves symmetrically 2-lobed to 0.2–0.4 (in ours), or strongly asymmetric and with a reduced or vestigial dorsal lobe; lobes ending in crescentic slime papillae attached along their longer walls, or without these cells (our species). Cells very large, leptodermous; surface smooth. Oil-bodies (Schuster, 2000a) glistening and almost homogeneous or, at most, obscurely botryoidal. Underleaves small or vestigial. Asexual reproduction absent.

Dioecious, autoecious (in ours), or paroecious. Androecia sometimes terminal but becoming intercalary on leading leafy axes, or sometimes on small, ventral-intercalary branches;

bracts pouched at base, bilobed; antheridia 1 per bract, the stalk uniseriate. Gynoecia normally on feeble, short, ventral-intercalary branches; bracts and bracteoles of innermost series bifid to 0.5–0.85, the lobes entire or subentire. Perianth fusiform-trigonous, the basal cells much larger than median and apical cells, the mouth narrow, deeply 6-fid; perianth 1-stratose.

Seta with 8 rows of large outer cells surrounding 4 rows of internal cells. Capsule wall 2-stratose; outer layer of cells rectangular, usually both faces of alternating walls with sinuous-nodular thickenings; inner layer of cells with well-defined semiannular bands.

Spores delicately areolate.

Type: *Zoopsidella cynosuranda* (Spruce *ex* Steph.) R.M.Schust. (≡ *Zoopsis cynosurandra* Spruce *ex* Steph.)

A genus of 8 species, of which only one occurs in New Zealand. The other species are Neotropical and range north to the Antilles; for these see Schuster (1999b). The genus has three subgenera: subg. *Hyalolepidoziopsis* R.M.Schust., with only our species, subg. *Hypozoopsis* R.M.Schust. and subg. *Zoopsidella*.

All species of *Zoopsidella* have large, flat, lamelliform leaves, unlike a number of *Zoopsis* species, in which leaves are usually highly reduced to a very few, specialized cells. Also, *Zoopsidella* has a seta of the 8+4 type vs. a seta with 8 epidermal cell rows enclosing numerous, much smaller internal cell rows in *Zoopsis*.

References: Schuster (1999b, 2000a).

The species treatment is adapted, with considerable modification, from Schuster (1999b).

Zoopsidella caledonica (Steph.) R.M.Schust.

[Plate 8E, F; Fig. 113: 1, oil-bodies, p. 504]

Zoopsis caledonica Steph., Sp. Hepat. 6: 318. 1922. *Zoopsidella caledonica* (Steph.) R.M.Schust., Taxon 18: 57, 87. 1969. Type: New Caledonia, *Lerat*.

Zoopsis foliosa Herzog & E.A.Hodgs. in Zotov et al., Trans. Roy. Soc. New Zealand 68: 320. 1938, *nom. nud.* (cf. Schuster, 1963b, p. 274, 1999, p. 114; Scott, 1969, p. 169).

Plants loosely prostrate, light to whitish green, distinctly nitid when dry, medium, to 1.3 μm, flat. Branching irregular, sparing, the branches mostly ventral-intercalary; *Frullania*- and *Zoopsis*-type branches much less frequent, from both right- and left-hand sides of axis; stoloniform branches common. Stem with cortex in 6 rows of somewhat inflated, leptodermous cells, the 2 dorsal rows very large, the ventral 2 rows of cells notably smaller; medullary cells very small, in 7–13 rows. Leaves contiguous, with at most 1 cortical cell intervening between successive leaves on each side of axis; leaves flat, regularly widely spreading, nearly longitudinally inserted, leaving a broad strip of 2 cell rows leaf-free, rectangular-lingulate, for the most part nearly parallel-sided, but weakly tapering toward the apices, 180–280 μm wide × 450–700 μm long, symmetrically bilobed to 0.2–0.25; lobes (2)3–4-celled, typically ending in a short uniseriate row of 2 submoniliform, persistent cells, the apical cell of leaf lobes not modified into papillae; disc 4 cells wide throughout, ca. 5–6 cells high. Cells large, the size and shape uniform throughout disc, the median cells of the disc 55–75 μm wide × 75–100 μm long; surface smooth. Oil-bodies occupying significant portion of cell lumen, bunching up in differing parts of the cells, appearing packed in cell, hyaline and somewhat translucent, 8–

14 per leaf disc cell, smooth, but obscurely, irregularly and indistinctly segmented, the surface appearing irregularly pinched. Underleaves small, usually of 2 basal cells forming a vestigial disc, and 2 vestigial lobes, each of 1(2) inflated cells, ending in a slime papilla.

Autoecious. Androecia on small, spicate, ventral-intercalary branches, the branches at times crowded and in the axils of several successive underleaves; bracts in 3–6 pairs, weakly pouched at base, bilobed; antheridia 1 per bract, the stalk uniseriate. Gynoecia on weak, ventral-intercalary branches; bracts of innermost series oblong, bifid to 0.5–0.65, the disc only (1.5)2–3 cells high, the lobes lanceolate to acuminate, terminating in a uniseriate row of 2–5 cells, the lobe margins with 1–2 small teeth; bracteole bifid only to 0.35–0.45, otherwise similar to bracts. Perianth mouth deeply 6-lobed, the lobes acuminate to subcaudate, terminating in a uniseriate row of 3–4 strongly elongated cells, the terminal 1–2 cells (4–6:1), the uniseriate row supported by 2–4 laterally juxtaposed cells that are ca. 2:1 or less, the lobes entire, rarely with a tooth.

Seta with 8 rows of outer cells surrounding 4 rows of slightly smaller inner cells. Capsule ellipsoidal, the wall 2-stratose; outer layer of cells somewhat irregular, with two-phase development, the primary walls delimiting mostly subquadrate to short-oblong cells, each divided longitudinally and occasionally transversely, the secondary walls with rather few, confluent, nodular thickenings; inner layer of cells with rather few, weak, incomplete to complete semiannular bands.

Spores 13–15 μm in diam., with very low, furcate-anastomosing ridges imperfectly delimiting areolae. Elaters 7.5–9.5 μm wide, bispiral, the spirals 2.5–3 μm wide.

Distribution and Ecology: New Zealand: Stewart Island (100–530 m), South Island (0–720 m), North Island (180–540 m), Chatham Islands; New Guinea, New Caledonia, Fiji. In New Zealand known from Westland, Southern North Island (Tararua Ra.), Volcanic Plateau (Atiamuri), Auckland (Waitakere Ra.) and Northland EPs.

Broadly distributed in New Zealand, but local and abundant and common only in the montane forests of Westland. The species occurs over permanently damp peaty soil deep in humid, deeply shaded, protected, cave-like areas under tree masses (especially under *Metrosideros umbellata*) or deep in shaded pockets in forests usually of *Dacrydium cupressinum*, *Libocedrus bidwillii*, *Weinmannia racemosa*, *Metrosideros umbellata* and *Quintinia serrata*. It is associated with *Acromastigum colensoanum*, *Bazzania nitida*, *B. nova*, *Kurzia hippuroides*, *Leucobryum candidum*, *Mittenia plumula*, *Psiloclada clandestina*, *Rhizogonium distichum*, *R. pennatum*, *Saccogynidium australe*, *Tylimanthus diversifolius*, *Zoopsis argentea* var. *argentea* and *Z. ceratophylla*. Also on organic substrates such as the fibrous caudices of *Dicksonia squarrosa* or *Cyathea medullaris* (with *Calomnion complanatum* and *Marsupidium epiphytum*) or deep in recesses of rotted, fallen tree trunks. On Stewart Island (Mt. Rocky Track, 100 m), in a mixed broadleaf–podocarp forest dominated by *Weinmannia racemosa*, and also including *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Metrosideros umbellata* where in a shaded, protected hollow formed by tree buttresses. Also, notably at the Mt. Rocky summit area (530 m), deep in a shaded protected niche under tussock in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus*.

Comments: A distinct species that can be confused only with *Zoopsis ceratophylla* (p. 484), which it resembles in the symmetrical, elongated, bilobed leaves with the lamina formed of 4 cell rows. It differs in the narrowly oblong-lingulate leaves, consistently tapered to the sub-

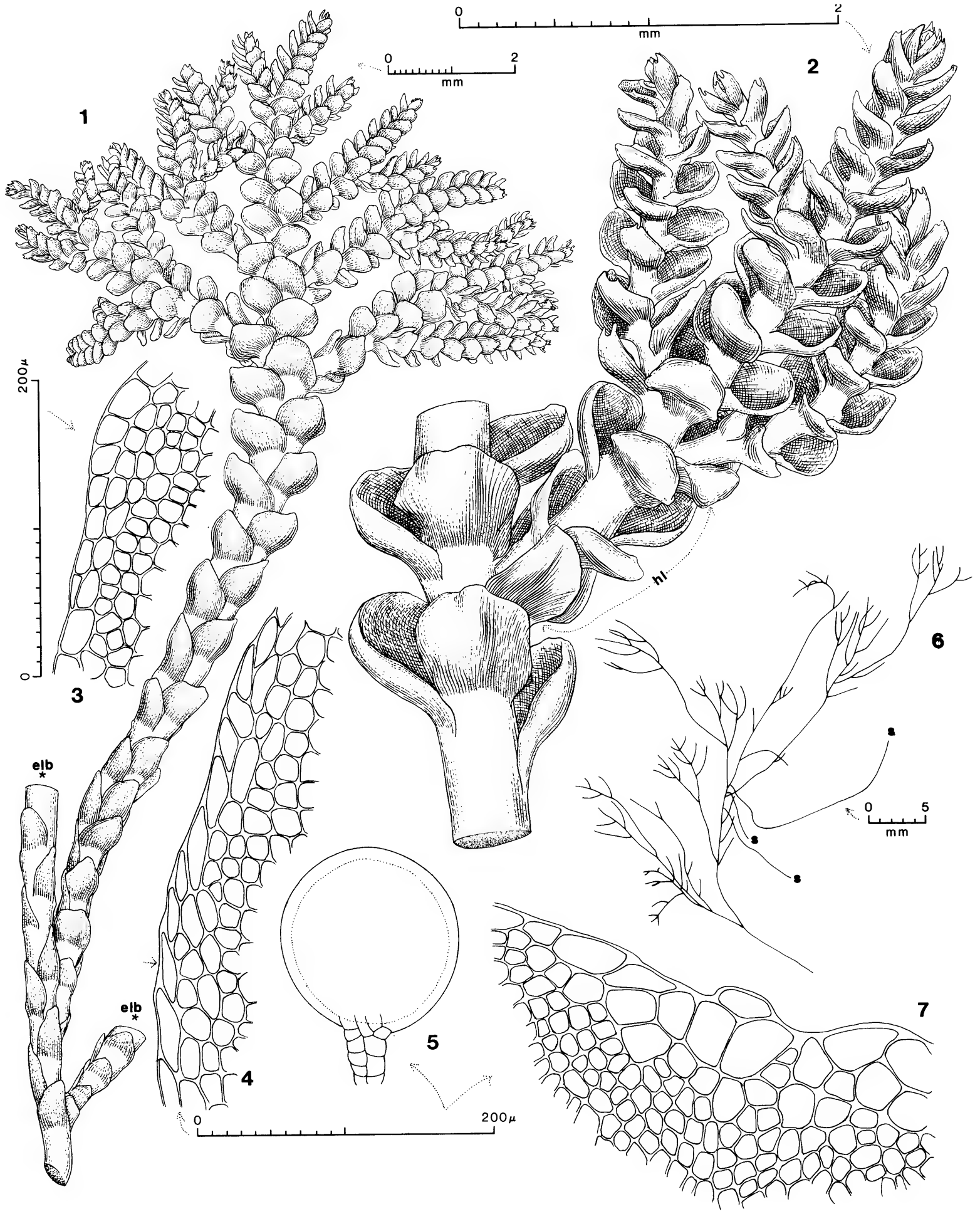

Fig. 111.
Isolembidium anomalum (Rodway) Grolle (fig. 5, from var. *cucullatum*, remainder from var. *anomalum*). 1. Erect leafy branch; 2 other erect leafy branches (= elb) truncated near their base (at *) (dorsal view). 2. Sector of erect leafy branch with a *Microlepidozia*-type primary branch (hl = half-leaf) and 3 secondary branches, the 2 at top of *Frullania* type, the one at bottom of *Microlepidozia* type (ventral view). 3. Leaf margin (median sector) showing border of larger cells (leaf removed from erect leafy shoot in zone with terminal branches). 4. Leaf margin (arrow indicates approximate midpoint of margin) showing ± optimal development of border of larger cells (leaf removed from same sector of shoot as in fig. 3). 5. Antheridium. 6. Cladograph (s =

parallel lobes that terminate in 1–2 cells that are not conspicuously moniliform, with the terminal cell never ending in a slime papilla. On the other hand, the leaves of *Z. ceratophylla* are narrowly oblong to obovate-cuneate, often widest in the distal half, with lobes that are somewhat spreading and terminate in a uniseriate row of (2)3–4(6) moniliform cells and the terminal cell at times is an unspecialized slime papilla. In *Zoopsidella caledonica* the cells of the lamina are conspicuously smaller and the oil-bodies are hyaline, smooth and almost homogeneous or only very faintly granular vs. opaque, rough, dull-surfaced and granular-botryoidal in *Z. ceratophylla*.

Schuster (1999b) erroneously stated that *Zoopsidella caledonica* is dioecious, but did not mention presence of androecia. The species is autoecious.

Subfam. ***Lembidioideae*** R.M.Schust.

Subfamily *Lembidioideae* R.M.Schust., Hepat. Anthocerotae N. Amer. 2: 11. 1969; *ibid*. 1: 382. 1966, *nom. nud*.

Isolembidium R.M.Schust.

Isolembidium R.M.Schust., Nova Hedwigia 15: 466. 1968; J. Hattori Bot. Lab. 26: 278. 1963, *nom. inval*.

Plants isophyllous, erect, plane or decurved to cernuous distally, green and opaque (olive-green in herb.), lacking conspicuous secondary pigments; shoots medium-sized, ca. 10–15 mm high, ca. 900–1050 μm wide. Branching frequent, irregular or regular, both intercalary and terminal; intercalary branches both ventral and lateral; terminal branches of *Frullania* and *Microlepidozia* types, issuing from distal sectors of shoots; older shoot-sectors conspicuously remote-leaved, with stems rhizome-like, extensively exposed and microphyllous—but a conspicuous system of geotropic stolons hardly developed (only occasional geotropic stolons seen). Stems with a distinct but not very pronounced hyaloderm that eventually collapses with age and 1–2 subepidermal layers of smaller, thick-walled, brownish cells and a medulla of numerous hyaline, rather leptodermous cells, the internal medullary cells larger. Rhizoids virtually absent. Leaves with insertion transverse to subincubous, broadly ovate-subrotundate to reniform-rotundate in outline, cucullate, nearly vertically oriented, obliquely to widely spreading above but appressed and ± clasping the stem toward shoot bases, firm, polystratose (median portions (2)3–4-stratose, only the margins thinner and gradually 1-stratose); apices undivided, variable: broadly rounded to repand to denticulate-dentate; margins entire. Cells firm, with walls thin to faintly thickened, but trigones conspicuous, although concave- to flat-sided; cells at leaf apex and often also along margins enlarged, hyaline, often eventually collapsing and then resulting in an erose condition; surface striolate-papillose. Oil-bodies absent in inflated cells at leaf apex, otherwise present in some cells while absent in others, occupying a very small portion of the cell lumen, smokey pale grey or hyaline, typically 1–2 (rarely

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stoloniform branch). 7. Portion of leaf apex showing field of enlarged cells. (Figs. 1–3, 7, from *Engel 14053*, Tasmania, Weindorfers Forest; 4, from *Scott*, Tasmania, Lake Pedder; 5, from *Oliver s.n.*, Auckland Is.; 6, from *Engel 20056*, Tasmania, West Coast Ra., Proprietary Peak.)

3–4) per median leaf cell, smooth and appearing without texture or finely and faintly granular, appearing nearly smooth, but obscurely and suggestively segmented (obscurely 3–4-segmented *fide* Schuster and Engel, 1987b), globose to narrow ovoid to narrowly to broadly elliptic to ± crescentic, 1.9–2.4 × 2.4–3.8 μm to, less often, 2.4 × 4.8 μm, spherical ones 2.9 μm in diam., the oil-bodies rather soon breaking up and, with breakup, becoming irregular, the surface appearing papillose and with discrete spherules. Chloroplasts large for cell size. Underleaves identical to leaves. Asexual reproduction lacking.

Androecia lateral- or ventral-intercalary in origin, basal, from leafy axes or microphyllous stolons, compactly spicate, julaceous, microphyllous, small, only 350–450 μm wide; bracts small, concave, rather boat-shaped, strongly inflated throughout, with sides folded together, the apex bluntly acute (when not flattened), undivided and entire; margins entire; antheridia 1 per bract, the stalk 2-seriate; bracteoles vestigial or reduced to few-celled remnants bearing several clavate slime papillae at apex, lacking antheridia. Gynoecia on abbreviated ventral-intercalary branches lacking normal leaves, the branches originating from lower sectors of upright leafy shoots; bracts and bracteole identical, erect, together tube-like and tightly ensheathing the lower sector of the perianth, deeply concave, much larger than leaves, elliptic to lingulate, the apex rounded to retuse, often with several slime papillae, the lamina margins with several slime papillae. Perianth exceedingly slender, terete below but trigonous above, very long (to 11.8× longer than wide) and extremely attenuated, narrow-fusiform, plicate toward the contracted, ± pointed apex, the mouth shallowly lobulate and crenulate with narrow, often curved cells that are barely free at the tips, the cells striolate-papillose.

Capsule long-cylindrical, the wall 4-stratose, 41–42 μm thick; outer layer of cells equal to thickness of 1.9–2.5 of interior strata, the radial walls with continuous sheets of magenta wall material plus weak nodular thickenings on both faces of alternating longitudinal walls; innermost layer of cells with semiannular bands, the bands thick, usually complete, the radial walls otherwise with continuous sheets of magenta wall material.

Spores 14.4–16.8 μm in diam., pale brown, with dense, low, but sharply defined papillae and short-vermiculate markings. Elaters rigid, nearly straight, bispiral, 11–13 μm in diam., the spirals 3.8–4.8 μm wide.

Type: *Isolembidium anomalum* var. *cucullatum* (E.A.Hodgs.) J.J.Engel & R.M.Schust. (≡ *Lembidium cucullatum* E.A.Hodgs.)

The genus is Australasian and has a single species with two varieties, both present in New Zealand.

References: Schuster and Engel (1987b; mon.); Schuster (2000a).

Isolembidium anomalum (Rodway) Grolle

[Figs. 111, 112; Fig. 113: 2, 3, oil-bodies, p. 504]

Lembidium anomalum Rodway, Tasman. Bryoph. 2: 70. 1916. *Isolembidium anomalum* (Rodway) Grolle, J. Bryol. 10: 264. 1979. Type: Tasmania, Cradle Mtn., *Rodway* (MANCH!).

Plants rather rigid, often circinate when dry in both field and herb., becoming brownish with age in herb. Branching variable in frequency (copious in var. *anomalum*); terminal branches irregular or regular and then 1–2(3)-pinnate; intercalary branches issuing from shoot sectors

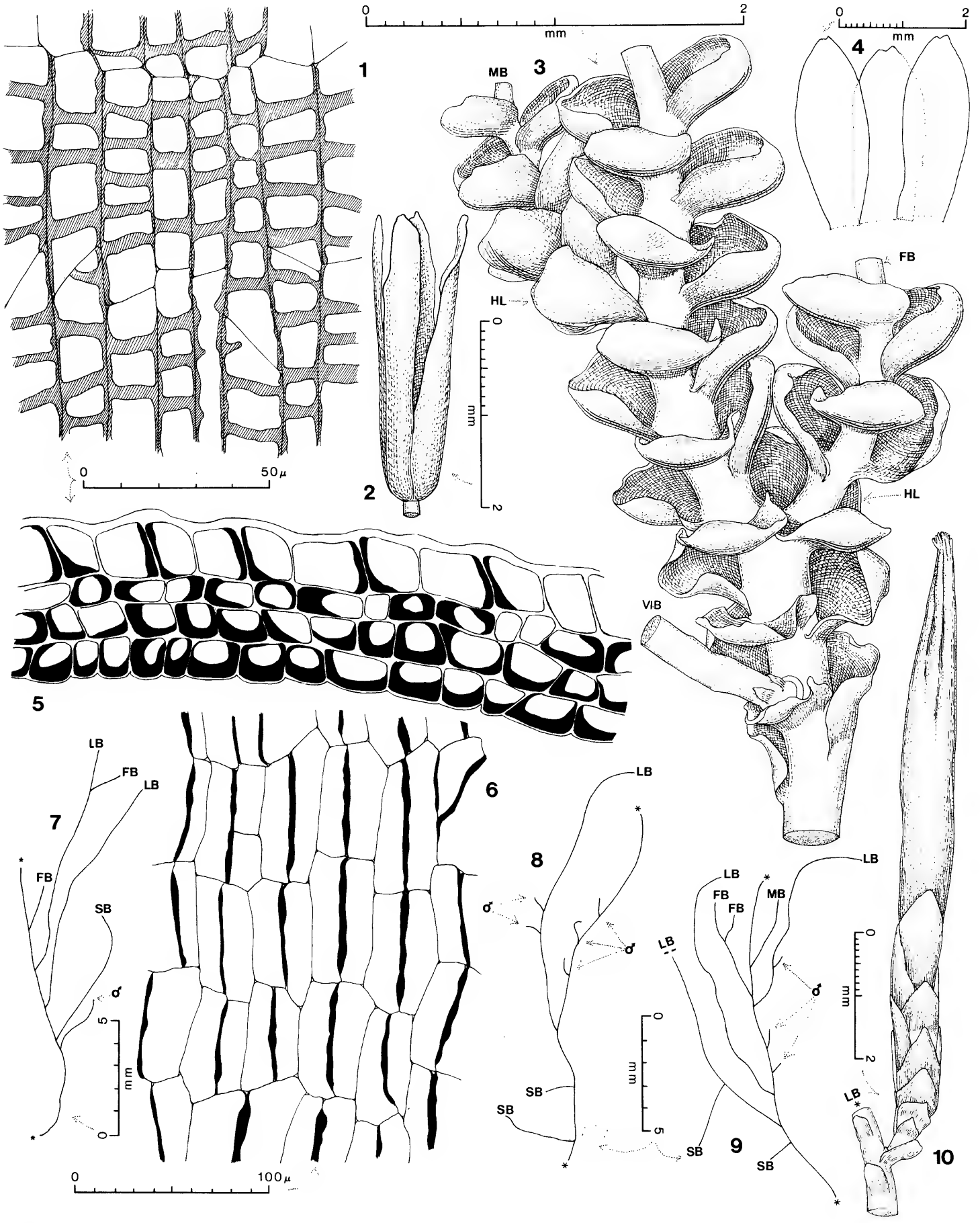

Fig. 112.
Isolembidium anomalum (Rodway) Grolle (figs. 3, 7–9, from var. *cucullatum*; 1, 2, 4–6, 10, from var. *anomalum*). 1. Capsule wall, inner layer. 2. Dehisced capsule. 3. Sector of erect leafy shoot with a *Microlepidozia*-type branch (= MB), and its associated half-leaf (= HL), a *Frullania*-type branch (= FB) and its associated half-leaf (= HL) and a ventral-intercalary branch (= VIB), ventral view. 4. Bracts and, in middle, bracteole. 5. Capsule wall, cross section. 6. Capsule wall, outer layer showing two-phase development. 7–9. Cladographs, the apex and base of the main shoot indicated with asterisks (♂ = androecial branch; SB = stoloniform branch; LB = erect leafy branch; FB = *Frullania*-type branch; MB = *Microlepidozia*-type branch; dash [--] = severed shoot). 10. Sector of upright leafy shoot with gynoecium; note perianth shape and closely ensheathing bracts (LB = erect leafy branch). (Figs. 1, 2, 4–6, 10, from *Engel 19535*, Tasmania, Weindorfers Forest; 3, 7–9, from *Oliver s.n.*, Auckland Is.)

basal to the terminal branches. Stems rather succulent (at least distally); cortical cells pellucid. Leaves and underleaves contiguous on mature shoot-sectors, at times ± canaliculate distally, almost impossible to flatten due to their hemispherical-cucullate form; apices rounded to subtruncate, often with a tear (when flattened). Cells at leaf apex swollen and 24–36(41) μm wide × 30–44(53) μm long, the remaining leaf cells rather small: subapical and median cells 12–20 μm wide × 13–24 μm long.

Androecial bracts rather antically assurgent, hyaline. Perianth with distal cells long oblong-rectangular, evenly thick-walled or with thickenings at the corners; mouth cells 12–16 × (54)60–90 μm, with evenly rather thick walls.

See key (p. 530) to distinguish this species from others in the family that produce upright, dendroid plants.

The species is subdivided into two varieties; both are represented in New Zealand:

Key to Varieties

1a. Terminal branching irregular, remote, sporadic on weaker plants, not aggregated to form a deltoid to subflabellate outline, the shoot apices usually straight, not decurved; branch leaves with apices consistently entire, edentate; stem with medulla 10–14 cells high. Campbell Is., Auckland Is., Stewart Is. . . . . var. *cucullatum* (p. 503)

1b. Terminal branching ± regularly 1–2-pinnate, the branches crowded toward the distal sector of leading shoots and defining a deltoid to subflabellate outline, the sector with terminal branches decurved to cernuous; branch leaves (particularly the narrower, more elongate ones of secondary and tertiary branches as well as distal sectors of primary branches) often with denticulate-dentate apices; stem with medulla 19–22 cells high. South Is. . . . . var. *anomalum* (p. 502)

Isolembidium anomalum (Rodway) Grolle var. ***anomalum***

[Fig. 111: 1–4, 6, 7; Fig. 112: 1, 2, 4–6, 10]

Plants decurved to cernuous distally. Terminal branching ± regular, 1–2(3)-pinnate, the branches crowded toward the distal sector of leading shoots and defining a deltoid to subflabellate outline; branch leaves (particularly the narrower, more elongate ones of secondary and tertiary branches as well as distal sectors of primary branches) often with denticulate-dentate apices. Stems rather stiff, in basal portion of well-developed shoots becoming ± woody, dark and brown and ultimately leafless with age; medulla 19–22 cells high.

Distribution and Ecology: New Zealand: South Island (60–600 m); Australia: Tasmania. Known in New Zealand from Canterbury (Arthur's Pass) and Western Nelson (Punakaiki, Stockton Plateau) EPs.

The typical variety is known from only a few South Island sites, e.g., in a pakihi 20 km N of Punakaiki at 60 m. At Arthur's Pass (Coral track, 600 m) it occurs on wet peaty soil in a forest of *Nothofagus solandri* var. *cliffortioides*, *Phyllocladus alpinus*, *Coprosma pseudocuneata* and *C. foetidissima*, with *Sphagnum falcatulum* and *Riccardia crassa*. At Stockton Plateau it occurs on Mt. Augustus at 960 m under *Metrosideros umbellata* and *N. menziesii* scrub on a granite rock outcrop, with *Adelanthus occlusus* and *Kurzia hippuroides*, and at Cypress

Stream (also Stockton Plateau, 700 m) under *Chionochloa juncea* and *Empodisma minus* tussockland, on soil with *Anastrophyllum schismoides*, *Dicranoloma robustum*, *Gackstroemia alpina* and *Riccardia crassa*.

Isolembidium anomalum var. ***cucullatum*** (E.A.Hodgs.) J.J.Engel & R.M.Schust.

[Fig. 111: 5; Fig. 112: 3, 7–9]

Lembidium cucullatum E.A.Hodgs., Rec. Domin. Mus. 4: 1. 1962. *Isolembidium cucullatum* (E.A.Hodgs.) R.M.Schust., Nova Hedwigia 15: 466. 1968. *Isolembidium anomalum* var. *cucullatum* (E.A.Hodgs.) J.J.Engel & R.M.Schust., J. Hattori Bot. Lab. 63: 268. 1987. Type: Auckland Is., above Musgrave Peninsula, Jan. 1944, *Oliver* (ex herb. Hodgson 11715) (MPN, *non vidi*); isotype (fragment): (F!).

Plants straight distally, not decurved. Terminal branching irregular, remote, sporadic on weaker plants, not aggregated to form a deltoid to subflabellate outline; branch leaves with apices consistently entire, edentate. Stems with medulla 10–14 cells high.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, Stewart Island (5 m); Australia: Tasmania.

This rare variety grows on Campbell Island usually as isolated stems in alpine moors, e.g., summit of Mt. Faye (Schuster, 2000a). On Stewart Island plants occur over a humus layer and dead debris under a dense layer of *Gleichenia* in a small open area among *Leptospermum scoparium* scrub in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium* – *Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus* (track to Mason Bay, ca. 1–1.8 km W of Freshwater Landing, 5 m).

Comments: A distinctive plant, readily recognized by its erect growth and triseriate shoots, with identical leaves and underleaves, which are strongly concave or even hooded at the apices. The opaque, undivided, polystratose leaves with a field of swollen cells at the apex are distinctive. The stem anatomy is also notable.

We are not certain that the two varieties will be able to be maintained when more collections come to hand. It is possible that var. *cucullatum* is merely a form of difficult conditions, e.g., exposed sites on Stewart Island or alpine areas. In both areas plants tend to occur as isolated individuals in a peaty low turf. Under such conditions, branching of the erect sectors of the gametophyte may be much reduced, so that the pinnate aspect fails to develop.

Lembidium Mitt.

Lembidium Mitt. *in* Hook.f., Handb. N. Zeal. Fl. 2: 751, 754. 1867, *nom. cons.*; Herzog, Ark. Bot. N.S. 1: 477. 1952 (1951), *p. p.*, subg. *Heterodictyon* only.

Plants strongly anisophyllous, erect, light to whitish green, secondary pigmentation lacking, moderate in size, to 1.6 mm wide, the leafy erect shoots with apices usually decurved, circinate or even hamate. Branching polymorphous: bearing ventral-intercalary, creeping, elongated and interwoven stolons in abundance; leafy branches erect, ventral-intercalary in origin from the felt-like mat of stoloniferous branches, the erect leafy axes sporadically to commonly branching, the branches of the *Frullania* type or sometimes ventral-intercalary; *Frullania*-type

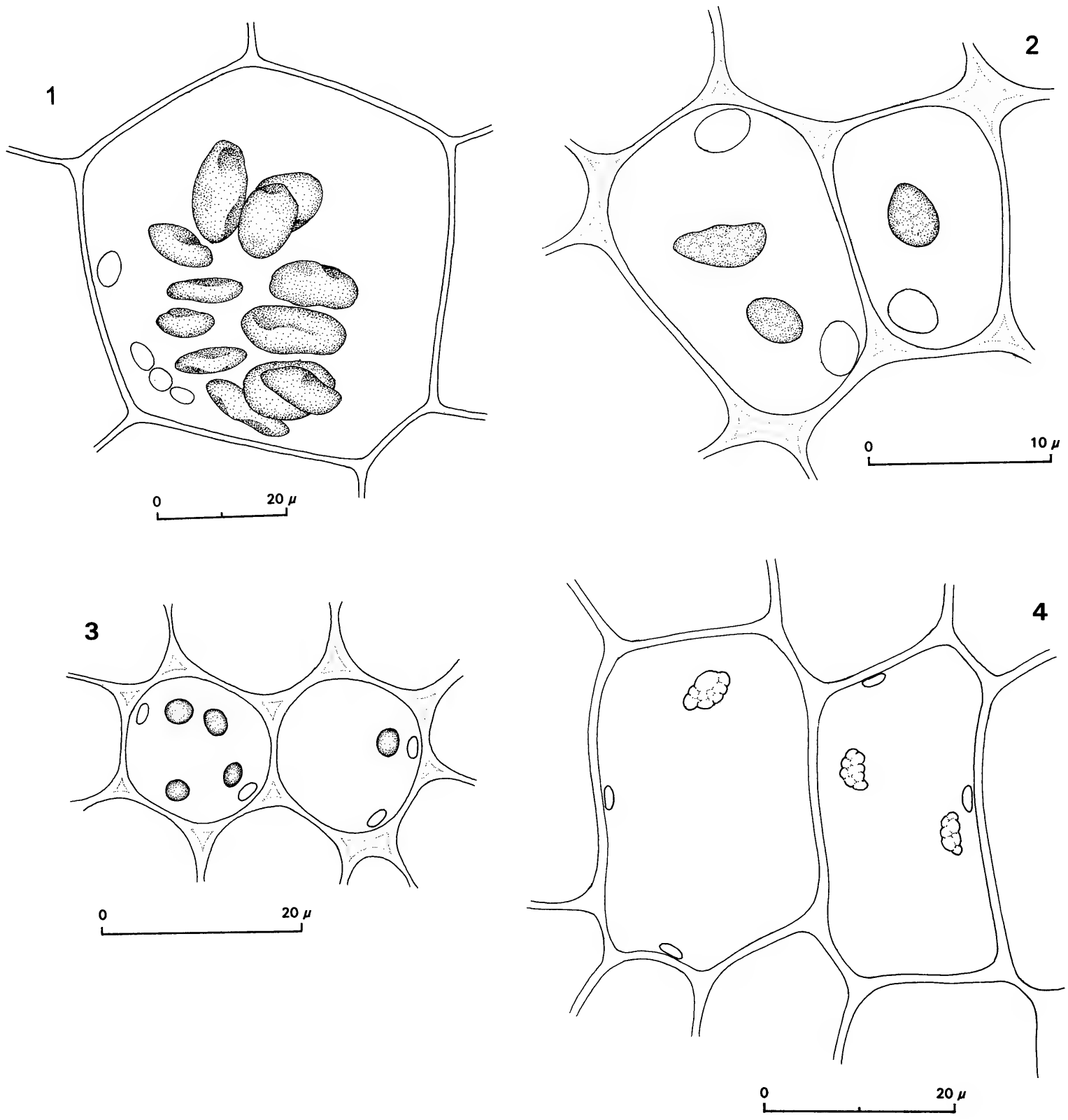

Fig. 113.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Zoopsidella caledonica* (Steph.) R.M.Schust. Disc cell at sinus base. 2. *Isolembidium anomalum* (Rodway) Grolle. Cells of median lamina of leaf, note that chloroplasts (not shaded) are ± size of the oil-bodies. 3. *Isolembidium anomalum* (Rodway) Grolle. Cells of median lamina of leaf. 4. *Hygrolembidium acrocladum* (Berggr.) R.M.Schust. Cells of lower-middle of leaf. (Fig. 1, from *Glenny 9099*, New Zealand, South Is., Westland EP, Mt. Brown; 2, from *Glenny 8911*, New Zealand, South Is., Western Nelson EP, Waimangaroa R., S end of Happy Valley (Cypress Stream); 3, from *Glenny 9350*, New Zealand, South Is., Western Nelson EP, Mt. Augustus; 4, from *Glenny 9399b*, New Zealand, South Is., Western Nelson EP, Brunner Ra.)

branches bazzanioid: from one side of axis only; lateral-intercalary branching apparently absent (at least in leafy shoot sectors). Stems of leafy shoots with cortical cells exceedingly large by comparison to leaf cells, the cortical cells often a little larger than the leptodermous medullary cells. Rhizoids lacking on erect, leafy shoots, present in small groups on stolons. Leaves distichous, rather widely laterally spreading, the insertion transverse to weakly or dis-

tinctly incubous, canaliculate-conduplicate, boat-shaped but without a keel, the dorsal halves lying slightly more displaced toward shoot apex than the ventral, incubously imbricate, the leaf thus with an incubous appearance in dorsal aspect, the leaves unistratose throughout; apices undivided and entire to emarginate or bidentate, or 4-dentate, or (3)4-lobate; leaf margins entire or irregularly toothed. Cells leptodermous throughout, at most the cells above the base with slight, evenly thickened walls; cells in basal area becoming very large, more inflated, forming a distinct area basalis, the cells of all but the area basalis relatively small, subquadrate to oblong to polygonal; surface papillose, the surface of area basalis cells smooth or striolate or papillose. Oil-bodies totally lacking in both leaf and stem cells; oil-droplets present in some populations of *Lembidium nutans*, tiny, homogeneous. Underleaves conspicuous throughout, ca. 0.5 the width and 0.3 the area of the lateral leaves, the apices crenulate-denticulate to shallowly or deeply bilobed. Asexual reproduction absent, or (*L. longifolium*) via caducous leaf lobes.

Androecia (known only for *Lembidium nutans*) on short, apparently always ventral-intercalary branches from near the bases of erect, leafy stems or from stolons, short and spicate; bracts ovate, inflated; antheridia 1(2) per bract, the stalk rather short, uniseriate; bracteolar antheridia rare. Gynoecia on very short, apparently ventral- or lateral-intercalary branches, from ± fleshy, microphyllous shoot bases. Gynoecial bracts in 3 series, gradually larger, imbricate, those of innermost series lanceolate to narrowly ovate-lanceolate, tapered to a narrow, pointed or bidenticulate tip; upper margins and apex with ± crenulate margins by free ends of elongated cells, otherwise entire. Perianth exceedingly slender, trigonous, very long (ca. 7× longer than wide) and extremely attenuated, fusiform, the apex shallowly to obscurely lobulate and crenulate with narrow, often curved cells that are somewhat thick-walled and free at the rounded, finger-like tips (or occasionally a few cells wholly free), the cells distinctly papillose (although perianth below apex is smooth).

Sporophyte known only in *Lembidium nutans*. Seta formed of 8(9) rows of very large outer cells surrounding a core of numerous, much smaller cells. Capsule long-ellipsoidal, ranging from 350 × 1120 μm to 560 × 1400 μm, the wall (2)3-stratose; outer layer of cells with nodular (radial) thickenings of, generally, both faces of alternating longitudinal walls, the thickenings ± confluent to form continuous sheets; innermost layer of cells with semiannular bands, the bands usually complete.

Spores 12.5–14.4 μm in diam., dark yellowish brown, rather coarsely papillose, with short irregular papillae coalescing to form clumps or short ridges that rarely delimit areolae. Elaters rigid, ± straight, 8.6–11.5 μm wide, slightly tapering toward tips, bispiral to tips, the spirals 3.8–4.8 μm wide.

Type: *Lembidium nutans* (Hook.f. & Taylor) Mitt. (≡ *Jungermannia nutans* Hook.f. & Taylor)

A genus with only two species, both found only in New Zealand.

References: Schuster and Engel (1987b; mon.); Schuster (2000a).

Key to Species

1a. Leaves relatively short, appearing inflated, without a discernible median longitudinal "keel," with apices unlobed and entire to 2–4-dentate; leaf margins untoothed or with an isolated few-celled tooth; plants whitish green, the leafy shoots erect from a stolonifer-

ous base; leafy shoots simple or sporadically with a single *Frullania*-type branch; shoot tips cernuous; cells of leaves strikingly dimorphic: basal cells inflated, smooth or striate, very large (ca. 25–60 × 70–120 μm), contrasted to distal and lateral cells, which are very small (ca. 16–22 × 20–26 μm), thick-walled and papillose; underleaves suborbicular, not strikingly bifid, the disc margins unarmed . . . . . *L. nutans* (p. 508)

1b. Leaves strongly elongated, folded-canaliculate and the lateral half of a canoe in form, with apices clearly (3)4-lobed; leaf margins sinuous and irregularly toothed and rather ragged; plants bluish green in life, the leafy shoots loosely to closely adnate to substrate; leafy shoots with 1–2(4) terminal branches all originating from one side of stem; shoot tips virtually straight; cells of leaves not sharply dimorphic: basal cells not inflated, gradually larger toward base (ca. 16–25[32] × 38–62[82] μm), the subapical cells slightly narrower (ca. 15–21 × 20–28[45] μm), the cells all rather thin-walled, all densely papillose; underleaves elongated, with 2 drawn-out apical lobes, the disc margins armed with several cilia . . . . . *L. longifolium* (p. 506)

Lembidium longifolium R.M.Schust.

[Plate 10B, C]

Lembidium longifolium R.M.Schust., Phytologia 45: 420. 1980. Type: New Zealand, North Is., Little Barrier Is., Summit Track of Mt. Hauturu, SE of summit of Mt. Herekohu, 1700–1900 ft., *Schuster 51446*.

Plants dull-textured, light bluish green (in herb. the older portions fading to ivory-white or tawny), creeping; leafy shoots to 1.6 mm wide, strongly dorsiventrally compressed, densely leafy and pectinate-distichous, the shoot tips somewhat (often feebly) cernuous. Branching common, the leafy axes arise from, and give rise to, microphyllous to virtually leafless, rhizoid-bearing whitish stolons and flagella, the leafy axes simple or, more often, bearing 1–2(4) *Frullania*-type leafy axes arising only from one side of main axis. Branches of leafy shoots mostly of *Frullania* type, rarely more than 1–2 per leafy, erect axis, arising via an acute bifurcation but with leading axis retaining its dominance, the branch laterally displaced. Stems of leafy shoots soft-textured, somewhat fleshy; cortical cells large, thin-walled, hyaline (lateral cortical cells in surface view very large, in 2–3 tiers between each pair of leaves, in stem cross section in 15–16 rows, the dorsal moderately thick-walled, not differentiated in cross section from medullary cells; medullary cells rather leptodermous; surface of cortical cells smooth in sharp contrast to the strongly and closely papillose basal leaf cells. Leaves contiguous-imbricate in 2 sharply defined ranks, spreading at nearly right angles (but the apical sectors again arched forward), strongly elongated, to 650–725 μm long, or more, folded-canaliculate so that they cannot be artificially flattened, shaped somewhat like the lateral half of a canoe, basically narrowly ovate in outline, orientation almost vertical, but so oriented that the leaves are clearly incubous, the leaves in antical aspect clearly incubously inserted; apices convergent, loosely folded (U-shaped in cross section), consistently (3)4-lobed for 0.18–0.24 their length, the lobes tapered, long-acute; leaf margins sinuous and irregularly paucidentate, the teeth very variable, sharp and oblique and 1–3-celled to spreading or recurved, the short cilia formed of 1–2 elongated cells; antical leaf bases typically with 1–2 often arched or reflexed, 1–2-celled cilia. Cells thin- to very weakly and equally thick-walled, all strongly and closely to contiguously papillose, the papillae subspherical, readily detached, mostly high and rounded; cells of lamina, from apical lobes to antical and postical bases, rather uniform in size and shape, mostly subquadrate to polygonal, occasionally (usually locally and sporadically)

moderately elongated, 15–21 μm wide × 20–28(45) μm long; laminar cells peripheral to base gradually grading into a small basal region of enlarged, but not inflated cells, the largest of which (in basal 1–3-celled tiers) range to 16–25(32) μm wide × 38–62(82) μm long; basal cells closely papillose like other leaf cells, but the papillae often rather elongated and lower. Underleaves narrower than stem, closely to loosely appressed, moderately concave, contiguous below to imbricate above, rather narrowly ovate, typically 0.25–0.35 bifid, sometimes with one, or less often both lobes reduced to 2–4-celled cilia, the lobes and/or cilia acuminate to long-acute; underleaf margins armed, like leaf margins, with irregular, chiefly 1–2-celled, often reflexed (especially near underleaf bases) teeth and short cilia. Asexual reproduction by caducous lobes of leaves. Otherwise unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (40–80 m), North Island (400–750 m), Chatham Islands. Known from Westland, Western Nelson, Volcanic Plateau and Auckland EPs.

The species has a sporadic distribution, occurring from Haast Pass north to the northern sector of Westland and in the North Island from the Herangi Ra. (ca. 720–750 m) north to the Kaimai Ra. (400–425 m) and Coromandel Forest Park (510–540 m); also on Little Barrier Island (type). A characteristic niche is that of shaded vertical banks (usually associated with streams) and cliff faces. For example, it is associated with *Paracromastigum furcifolium* on the concave portion of the lip at the upper extreme of a deeply shaded vertical bank, the lip formed by the forest edge above. The station is in a stream valley under *Beilschmiedia tawa* and *Weinmannia silvicola* with a subcanopy of *Schefflera digitata*, *Cyathea dealbata* and *C. smithii* and a shrub layer of *Freycinetia baueriana* and *Cortaderia* (Kaimai Ra., headwaters of Poupou Stream). In the Herangi Ra. it formed large patches on a bryophyte-covered vertical, moist, south-facing cliff of ca. 5 m high (S of Te Whakapatiki, W of Te Kuiti). On Little Barrier Island occurring on a shaded, moist, very sheltered cliff face in the transition from *Agathis australis* forest to *Beilschmiedia tawa – Weinmannia silvicola* forest (520–580 m, type), admixed with *Hymenophyllum ferrugineum*. In the South Island it has been found under *Weinmannia racemosa*, *Nothofagus solandri* and *N. truncata* forests with associated species *Balantiopsis convexiuscula*, *Hymenophyllum sanguinolentum*, *Hypnodendron arcuatum*, the creeping vine *Metrosideros diffusa*, *Mittenia plumula*, *Psiloclada clandestina*, *Saccogynidium australe*, *Sticta filix*, *Telaranea herzogii*, *T. tuberifera*, *Zoopsis leitgebiana* and *Z. setulosa*.

Unlike *Lembidium nutans*, this species occurs only in exceedingly densely shaded sites, typically in deep, dark recesses or cave-like sheltered places, where humidity is high, but plants are sheltered from direct rain.

Comments: The dull, slightly bluish green color, the almost velvety texture and the very compressed shoots are diagnostic. *Lembidium longifolium* is strikingly different from *L. nutans*, chiefly in 1) the narrower leaves, with the shoots thus appearing more compressed; 2) the tendency for the leaves to be very conspicuously lobed at the apex and for the margins to bear several irregular, jagged teeth; 3) the leaf cells more nearly uniform throughout the leaf, without a prominent basal zone of conspicuously enlarged, inflated, smooth cells; 4) exceedingly closely papillose surface, with the rounded papillae easily detached when leaf cross sections are cut; and 5) underleaves always narrower than the stem, ovate from a broad and truncate base and usually clearly bilobed at the narrowed summit, the lobes and/or lateral flanks typically bearing 1–several conspicuous teeth or cilia. Leafy shoots are much more frequently branched than in *L. nutans* and the branches always are formed only along one side of the main axis, just as in *Bazzania*.

Lembidium nutans (Hook.f. & Taylor) Mitt.

[Plate 10A]

Jungermannia nutans Hook.f. & Taylor, London J. Bot. 3: 389. 1844. *Mastigobryum nutans* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 219. 1845. *Micropterygium nutans* (Hook.f. & Taylor) Mitt. *in* Hook.f., Bot. Antarc. Voy. 2: 148. 1854. *Bazzania nutans* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 414. 1877. *Cephalozia nutans* (Hook.f. & Taylor) Spruce, Cephalozia 97. 1882. *Lembidium nutans* (Hook.f. & Taylor) Mitt. *in* A.Evans, Trans. Connecticut Acad. Arts Sci. 8: 266. 1892. Type: Auckland Is., *Hooker* (G!).

Plants pale, whitish green, water-repellent, quite opaque when dry, when wet becoming pellucid; leafy shoots 1.1–1.6 mm wide × 7–12 mm high, often circinate or hamate. Leafy branches sporadic to rather common, the branches mostly terminal, of the *Frullania* type and 1(2) per leafy shoot, or sporadically ventral-intercalary. Stems of leafy shoots fleshy, of leptodermous cells throughout, quite pellucid, virtually echlorophyllose, the epidermal cells with diffuse chloroplasts; cortical cells strongly elongated, narrowly oblong; lateral merophytes formed of 2–3 tiers of cortical cells. Leaves contiguous to distinctly imbricate, inflated in aspect, not folded-canaliculate and without a discernible "keel" between halves of the leaf, broadly ovate to ovate-rotund when flattened, the insertion transverse to weakly incubous; apices undivided and entire to emarginate or bidentate or quadridentate; margins entire or crenulate through projecting cells, or occasionally with an isolated tooth terminating in a slime papilla; leaves with a distinct basal area of much larger, more inflated, pellucid cells, the peripheral cells relatively small. Cells bulging or strongly convex in leaf profile, rather small, 16–22 × 20–26 μm, in the area basalis becoming pellucid, swollen and very large, from a minimum of 25–30 × 70 μm to 45–60 × 80–120 μm; cells very slightly chlorophyllose, the cells of the area basalis hardly so; surface of area basalis cells smooth or striolate, the surface of peripheral cells and elsewhere papillose. Oil-droplets present in some populations, tiny, homogeneous. Underleaves ± imbricate, transversely inserted, ovate to rotund-ovate; apices crenulate-denticulate to shallowly bilobed; disc margins entire. Fungal partner absent.

Gynoecia with innermost bracts lanceolate to narrowly ovate-lanceolate from a broad, truncate base, large-celled, hyaline, thin, tapered to a narrow, pointed or bidenticulate tip; upper margins and apex ± crenulate marginally with free ends of elongated cells, otherwise entire. Perianth tapering in the distal 0.35–0.4 to a conical, almost pointed tip, the perianth formed of exceedingly large, thin-walled, oblong cells; mouth cells from 55–60 × 13–17 μm to 80 × 13 μm.

Sporophyte details in the generic description above.

Distribution and Ecology: Endemic to New Zealand: Campbell Island, Auckland Islands, Stewart Island (10–530 m), South Island (10–1140 m), North Island (170–1100 m). Known from Fiordland, Otago, Westland, Canterbury, Western Nelson, Southern North Island, Taranaki, Gisborne, Volcanic Plateau, Auckland and Northland EPs.

Unlike *Lembidium longifolium*, which inhabits only very sheltered sites, *L. nutans* tends to be a pioneer (particularly over clayey soil) on relatively well-illuminated banks, paths and road cuts, where sporadic desiccation occurs. The extensive system of subterranean rhizoidous axes may be of significance in consolidating roadside and trackside banks, a characteristic habitat of the species. The species at times may occur in sheltered niches, but these differ from those characteristic of *L. longifolium*. For example, *L. nutans* occurred on the ventral-lateral side of a rotted, decorticated log in a wet mossy forest of *Lepidothamnus intermedius*, *Ixerba*

brexioides and *Dacrydium cupressinum* with occasional *Phyllocladus glaucus* (summit of Table Mtn., Coromandel Forest Park, 835 m). Also forming a solid patch in a mound of *Balantiopsis tumida* at the edge of a narrow, shallow, stagnant pool with saturated, rich, peaty soil in a mixed podocarp–broadleaf forest, the vegetation consisting of *Dacrydium cupressinum*, *Weinmannia racemosa* and *Podocarpus totara*, with an open understory dominated by *Pseudowintera colorata* (Lake Kaniere Scenic Reserve, Westland, 125 m). In the penalpine zone on soil banks under *Olearia colensoi* scrub and *Chionochloa pallens* tussockland. Accompanying species are *Balantiopsis diplophylla*, *Distichophyllum pulchellum*, *D. rotundifolium*, *Ditrichum difficile*, *Fissidens pallidus*, *Hygrolembidium australe*, *Lepidozia pendulina*, *Leucobryum candidum*, *Pallavicinia xiphoides*, *Riccardia colensoi*, *R. crassa*, *Sticta filix* and *Telaranea lindenbergii*.

Comments: *Lembidium nutans* is a most peculiar plant. The erect, often crowded, pale to whitish green leafy shoots are quite distinctive, with their contiguous-imbricate, hollowed-out, distichous leaves. These shoots are always of very limited and finite height and arise from a system of whitish, flagelliform axes that may penetrate the substrate for 2–3 cm, if not more. The plant does not have the facies of a member of the *Lepidoziaceae*, although the occasional occurrence of a terminal, *Frullania*-type branch, associated with the ventral, long stolons and the restricted rhizoids are "lepidozioid" features. The total lack of oil-bodies is notable. Unlike *L. longifolium*, which has more flattened shoots with weakly decurved tips, *L. nutans* has diagnostically cernuous shoot apices, as the species name suggests. Most similar in appearance to *Chloranthelia berggrenii* and the two may be found in similar habitats, but *L. nutans* lacks the obvious teeth on the leaf margins of that species. Similar to *Hygrolembidium acrocladum* and *H. australe*, which occur in similar habitats, but the leaves of *L. nutans* are opaque, whereas those two species have translucent leaves.

Hygrolembidium R.M.Schust.

Lembidium subg. *Isodictyon* Herzog, Ark. Bot. N.S. 1: 479. 1952 (1951), *p. p.*
Hygrolembidium R.M.Schust., J. Hattori Bot. Lab. 26: 277. 1963.

Plants isophyllous to clearly anisophyllous, erect, clear green (without ability to develop secondary pigmentation), translucent or opaque. Branching exclusively intercalary, from axils of both leaves and underleaves, the leafy branches erect, straight; stolons generally freely developed, prostrate, freely branched, long, slender. Stem soft and ± fleshy, without a hyalodermis; cortical cells thin- or feebly thick-walled, averaging smaller than medullary cells (in ours); medullary cells leptodermous (in ours). Rhizoids of leafy branches issuing from basal cells of underleaves (and sometimes also of leaf) or from stem at immediate base of foliar tissue; rhizoids more regularly produced on stolons. Leaves concave to cupulate, commonly fleshy, at least the basal area 2–7-stratose, the insertion transverse to distinctly succubous; apex broadly rounded to retuse or incised, unlobed. Cells of leaf apices sometimes equally thick-walled, but at least in median and basal sectors of leaves (areas of 2 or more strata) leptodermous and without trace of trigones, the cells not enlarged; surface (at least of marginal and subapical cells) often ± papillose; median and basal, chlorophyllous cells with small, inconspicuous, glistening oil-bodies 1–2(3) per cell in isolated epidermal cells, the oil-bodies absent in many (in *Hygrolembidium rigidum* in essentially all) cells, some hypodermal cells with 3–9 similar, small, few-segmented oil-bodies. Underleaves distinct, ranging from 0.1–

0.9 area of lateral leaves; apex undivided and crenulate to retuse to shallowly bifid; lamina margins feebly dentate. Asexual reproduction lacking.

Dioecious. Androecial plants often much smaller than ♀ plants; androecial branches either lateral- or ventral-intercalary in origin, spicate, sometimes proliferating vegetatively distally but never with vegetative leaves basal to androecium on a branch; bracts much smaller than leaves, very strongly saccate, bearing 1–4 antheridia each; antheridia with stalk 2–4(or more)-seriate; bracteolar antheridia lacking (except *Hygrolembidium australe*, where occasional). Gynoecia on short, abbreviated, intercalary branches lacking normal leaves, the branches either from axils of lateral leaves, or from axils of underleaves; bracts inserted on a broad base, the apex grading from entire and merely with slime papillae to 2–4-dentate-lobulate to distinctly bifid; lamina margins dentate to ciliate or entire; bracteole identical or nearly so to bracts, or slightly smaller. Perianth 3(4)-gonous at least above (occasionally cylindrical throughout in *H. acrocladum*), pluriplicate distally, contracted to the crenulate to lobulate mouth; perianth 2–5-stratose at base thinning to unistratose toward mouth.

Seta with 10–20 large, outer rows of cells surrounding numerous rows of moderately smaller internal cells. Capsule ellipsoidal to ovoid, the wall 3–5-stratose; outer layer of cells with one-phase development: with nodular thickenings on all or virtually all longitudinal radial walls (except *Hygrolembidium rigidum* where nodular thickenings weak or lacking), the transverse walls with nodular thickenings sparing to frequent; innermost layer with radial (vertical) bands nodular to spur-like in surface view, varyingly extended tangentially to form incomplete to complete, semiannular bands.

Spore wall with papillose to short-vermiculate markings.

Type: *Hygrolembidium stereophyllum* (Herzog) R.M.Schust. (≡ *Lembidium stereophyllum* Herzog)

The eight species of *Hygrolembidium* are chiefly Antarctic–subantarctic in range (one species, *H. isophyllum* R.M.Schust., occurs in Antarctica) and are present not only in continental areas (e.g., southernmost South America, *H. isophyllum*) but on most of the remote island regions (e.g., *H. ventrosum* (Mitt.) R.M.Schust. of Kerguelen, Crozet Island and Marion Island) including geologically recent, volcanic island groups. One species, *H. andinum* (Herzog) R.M.Schust., occurs in the Andes of central Chile and Venezuela and another, *H. boschianum* (Sande Lac.) R.M.Schust., occurs in Indo-Malaysia.

References: Schuster and Engel (1987b; mon.); Schuster (2000a).

Key to Species

1a. Plants subisophyllous to isophyllous, the underleaves at least 0.4 the leaf size, at times identical to leaves; leaf margins with teeth and slime papillae; leaf apices often with an incision or notch; antheridia 1 per bract axil; capsule wall outer layer with ± even, sheet-like thickenings well developed and nodular thickenings poorly so; inner layer of capsule wall rarely with complete semiannular bands. Subg. *Hygrobiellopsis* R.M.Schust. 2

2a. Leaves in basal cross section (2)3–4-stratose, the epidermal cells on average ± the same size as internal cells; cell width increasing from leaf apex to base, the basal cells to 3× the diam. of distal cells; surface of leaves papillose, at least in distal and marginal sectors . . . . . *H. rigidum* (p. 511)

2b. Leaves in basal cross section 5–7-stratose, the epidermal cells on average smaller in diameter than internal cells; cell width remaining nearly the same from leaf apex to base: 22–32 μm; surface of leaves smooth throughout . . . . *H. triquetrum* (p. 513)

1b. Plants clearly anisophyllous, the underleaves inconspicuous, never more than 0.25 the leaves in area and differing in form; leaf margins entire, without slime papillae; leaf apices usually broadly rounded or truncate, rarely and sporadically with a notch; antheridia 2–4 per bract axil; capsule wall outer layer lacking sheet-like thickenings but with nodular thickenings well developed; inner layer of capsule wall with well-developed semiannular bands. Subg. *Hygrolembidium* 3

3a. Cells of distal sector of leaf subquadrate, neither strongly elongated nor prosenchymatous; leaves orbicular to suboblate, occasionally ovate, with apices basically broadly rounded to truncate, never consistently bluntly acute . . . . . *H. acrocladum* (p. 517)

3b. Cells of distal sector of leaf strongly elongated (most 2–3:1, near margins distally even 3–6:1), ± prosenchymatous, cells of distal and marginal sectors thick-walled; leaves ovate-pointed, with bluntly acute, deeply concave tips, the larger with apices vaguely folded . . . . . *H. australe* (p. 521)

Subg. ***Hygrobiellopsis*** R.M.Schust. *ex* Bedn., Váňa, Ochyra & R.I.L.Sm.

Hygrolembidium subg. *Hygrobiellopsis* R.M.Schust., Nova Hedwigia 15: 467. 1968, *nom. inval.* Liverwort Fl. Antartica 56. 2000. Type: *Hygrolembidium isophyllum* R.M.Schust.

Hygrolembidium rigidum R.M.Schust. & J.J.Engel

Hygrolembidium rigidum R.M.Schust. & J.J.Engel, Phytologia 62: 9. 1987. Holotype: New Zealand, South Is., Fiordland Natl. Park, Mt. Burns, Hunter Mtns., 4500–5000 ft., *Schuster 84-101* (F); isotype: (CHR).

Plants fleshy and brittle, subisophyllous or underleaves only moderately smaller than leaves on the erect, ± triquetrous shoots, intense pure green, the leafy shoots to 1.8 mm wide. Branching common, the branches mostly ventral-intercalary, occasionally lateral-intercalary, very rarely of *Frullania* type; stolons sporadic or occasional, colorless, only rarely forming a freely branched prostrate system from which arise the erect leafy shoots. Stem very thick for plant size, formed of up to ca. 50 rows of cortical cells that are thin-walled (except free walls faintly thickened), variable but rather small. Rhizoids occasionally toward base of erect, leafy shoots, from basal cells of underleaf or leaf or from stem at immediate base of foliar tissue. Leaves firm, rigid, opaque, often ± keeled below, polystratose over 0.6–0.8 their area, only marginal and distal sectors unistratose; leaves in cross section toward base (2)3–4-stratose in intramarginal sector, the leaves remaining polystratose to at most within 2 cells of margin, the marginal sector unistratose, the epidermal cells of leaf averaging ± the same size as internal cells; leaves contiguous to moderately imbricate, widely spreading, transverse to feebly succubously inserted, deeply concave to subcupulate to subcanaliculate, broadly ovate-triangular to reniform-orbicular to oblate, 860–1525 μm wide × 665–1155 μm long when flattened; apex somewhat narrowed, usually with a sharp, short incision or at least retuse, sometimes 3–4-lobulate and/or dentate, often loosely folded or canaliculate; lamina margins entire or often repand to repand-dentate, slime papillae frequent. Cells showing gross size increase from api-

cal and marginal areas (here 20–25 × 24–30 μm to 24–35 × 28–48 μm) to base (here 40–60 × 55–85 μm to 60–85 × 70–100 μm up to 45–60 × 100–120 μm); cell walls thin throughout, distally with at most medium-sized trigones; surface obscurely to distinctly papillose throughout leaf, only the median or median-basal cells sometimes smooth. Oil-bodies completely lacking, only a few scattered, tiny, glistening oil-droplets present. Chloroplasts numerous, small: 1.4–2.4 × 2.4–4.3 μm. Underleaves 0.4–0.65(0.75) as large as leaves, ovate-triangular to orbicular-reniform to broadly ovate-reniform, usually folded-canaliculate; apex often retuse or shallowly bifid; lamina margins entire or repand, often with slime papillae.

Androecia on both lateral- and ventral-intercalary branches; bracts erect, the apex crenate-denticulate; antheridia single per bract, the stalk bistratose throughout or unistratose but with bistratose areas. Gynoecia mostly ventral in origin, occasionally lateral; bracts and bracteoles nearly identical (except bracts somewhat falcate), sheathing only basal ca. 0.25 of perianth and appressed to the perianth except for the slightly patent tips, somewhat larger than leaves, concave, ovate from a broad base, the apex blunt to narrowly truncate or subacute, unlobed, with armature as in perianth mouth; lamina margins dentate to ciliate, slime papillae common. Perianth exceptionally long for plant size, to 6 mm long × 1.2 mm in diam., long-fusiform, cylindrical below and bluntly 3(4)-gonous above, the mouth crenate-denticulate with thin-walled, laterally connate, finger-like cells that are mostly 3.5–5:1 and 10–18 × 45–55(65) μm; perianth 3–5(6)-stratose at base.

Seta with 10–14 rows of epidermal cells. Capsule long-ellipsoidal (2.6–3.5× as long as wide), the wall 3(very locally 4)-stratose, 46–48 μm thick; outer layer of cells with longitudinal and some transverse walls with thin to moderately thickened continuous sheets of wall material but with nodular thickenings weak or lacking (primary walls with thickenings often weaker or absent); innermost layer of cells with radial (vertical) bands nodular to spur-like in surface view, varyingly extended tangentially to form incomplete to complete, semiannular bands.

Spores 12.4–13.5 μm in diam., the wall yellow-brown, with low, delicate papillose and simple or sometimes furcate vermiculate markings, 1.3–1.5× the elater diam. Elaters faintly tortuous, bispiral, 8.6–9.6 μm wide, the spirals 2.9–3.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (660–1330 m). Known from Fiordland, Westland and Western Nelson (Paparoa Ra., Stockton and Denniston plateaus, Cobb Valley) EPs.

The species typically occurs in penalpine areas of *Dracophyllum* and *Olearia colensoi* scrub or *Hebe* and *Dracophyllum* scrub or in *Chionochloa pallens – C. flavescens* or *C. rubra* tussockland. In both scrub and tussockland it occurs over soil at bases of boulders, under overhangs, in pockets, as well as under tussock blade cover. Here it occurs, characteristically, with *Pachyschistochila*. Other accompanying species are *Andreaea acutifolia*, *Campylopus clavatus*, *Chloranthelia berggrenii*, *Cladia retipora*, *Cladonia confusa*, *Dicranoloma robustum*, *Jamesoniella colorata*, *Kurzia hippuroides*, *Pleuridium arnoldii*, *Racomitrium crispulum*, *Rhizocarpon geographicum*, *Riccardia cochleata*, *Siphula fragilis*, *Solenostoma totipapillosum* and *Verdoornia succulenta*. The species rarely occurs in *Nothofagus* forests (near South Branch of Borland Burn, Fiordland, 855–870 m) on soil of a bank above a cascading stream.

Comments: Distinctive for this species are the 1) very large basal epidermal leaf cells, contrasted to the much smaller distal cells; 2) lack of oil-bodies; 3) very thick and rigid stem; 4) lack of differentiation of epidermal and internal leaf cells as seen in leaf cross section; 5) frequently rather large underleaves, often similar to the leaves, so that the shoot is almost trigonous when looking down on the apex; and 6) unusually elongated, long-tapered and

fusiform perianth, which, in contrast to the fleshy stem and leaves, is exceptionally thin and delicate above, on old plants typically collapsed and browned. The thin and delicate, unusually small bracts and bracteoles are unlobed, edentate and somewhat asymmetrically ovate-pointed from a broad base. The species usually occurs in better-drained, less peaty habitats than *Hygrolembidium australe* and *H. acrocladum*. The species resembles a small *Pachyschistochila* but has larger underleaves than any species in that genus.

Hygrolembidium triquetrum J.J.Engel & R.M.Schust.

[Figs. 114, 115]

Hygrolembidium triquetrum J.J.Engel & R.M.Schust. *in* Schuster and Engel, Phytologia 62: 11. 1987. Holotype: New Zealand, South Is., Westland Prov., Mt. Aspiring Natl. Park, below and W of Mt. Armstrong, SSW of Mt. Brewster, 1250–1450 m, *Engel 17790* (F); isotype: (CHR).

Plants exceedingly fleshy and brittle, subisophyllous to ± isophyllous on the erect triquetrous shoots, pure green, the leafy shoots to 2.4 mm wide. Branching copious, both ventral- and lateral-intercalary; stolons colorless, common but not usually forming a freely branched prostrate system. Erect leafy shoots arising from stolons. Stem very thick for plant size, the cortex in ca. 65 rows of thin-walled cells, well differentiated, in 1 or locally 2 layers; medullary cells variable, distinctly larger than cortical cells. Rhizoids often toward base of erect, leafy shoots, from basal cells of underleaf or leaf or from stem at immediate base of foliar tissue. Leaves firm, rigid, brittle, opaque, often ± keeled below, very firmly attached at a thickened, fleshy base, polystratose for ca. 0.85 their area, only a few cell rows of marginal sector and several of distal sector unistratose; leaves in cross section toward base 5–7-stratose in intramarginal sector, the epidermal cells of leaf averaging considerably smaller than internal cells, those of abaxial face particularly so; leaves contiguous to moderately imbricate, orientation variable: suberect to widely spreading, transverse to faintly succubously inserted, moderately concave to cupulate to canaliculate, oblate to reniform, 1125–1225 μm wide × 850–900 μm long (to base of abaxial face) when flattened; apex variable, often broadly rounded to subtruncate, at times somewhat narrowed (particularly on smaller leafy branches), entire or sometimes with a few small teeth, sporadically retuse; lamina margins entire or often repand to repand-dentate, slime papillae frequent. Cell walls thin to slightly thickened, those of apical sector with at most medium-sized trigones, those toward base leptodermous, with trigones small or absent; cells of apical sector subquadrate, 23–31 μm wide and long; median cells 22–31 μm wide, 26–37(42) μm long; basal cells variable in shape: some short-rectangular or even subquadrate, others elongate, the cells 22–32 μm wide, 36–52 μm long; surface uniformly smooth. Oil-bodies not seen. Underleaves similar to leaves in form and often not or hardly differentiated from them, 0.5–0.75 as large as leaves to at times subequal to them, ovate to subreniform; apex plane to (often) hood-like, variable, undivided and entire or retuse to shallowly bifid; lamina margins entire or repand-dentate to dentate, often with slime papillae.

Androecia on both lateral- and ventral-intercalary branches, subjulaceous, vermiform, tiny for plant size, only 385–525 μm wide, colorless but with whitish antheridia, fragile and easily detached, often crowded toward base of erect, leafy shoots, also present (but less crowded) on stolons; bracts with apices and sides suberect, the apices crenate-denticulate; antheridia single per bract, the stalk biseriate. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (530 m), South Island (1250–1730 m). Known only from Rakiura and Westland EPs.

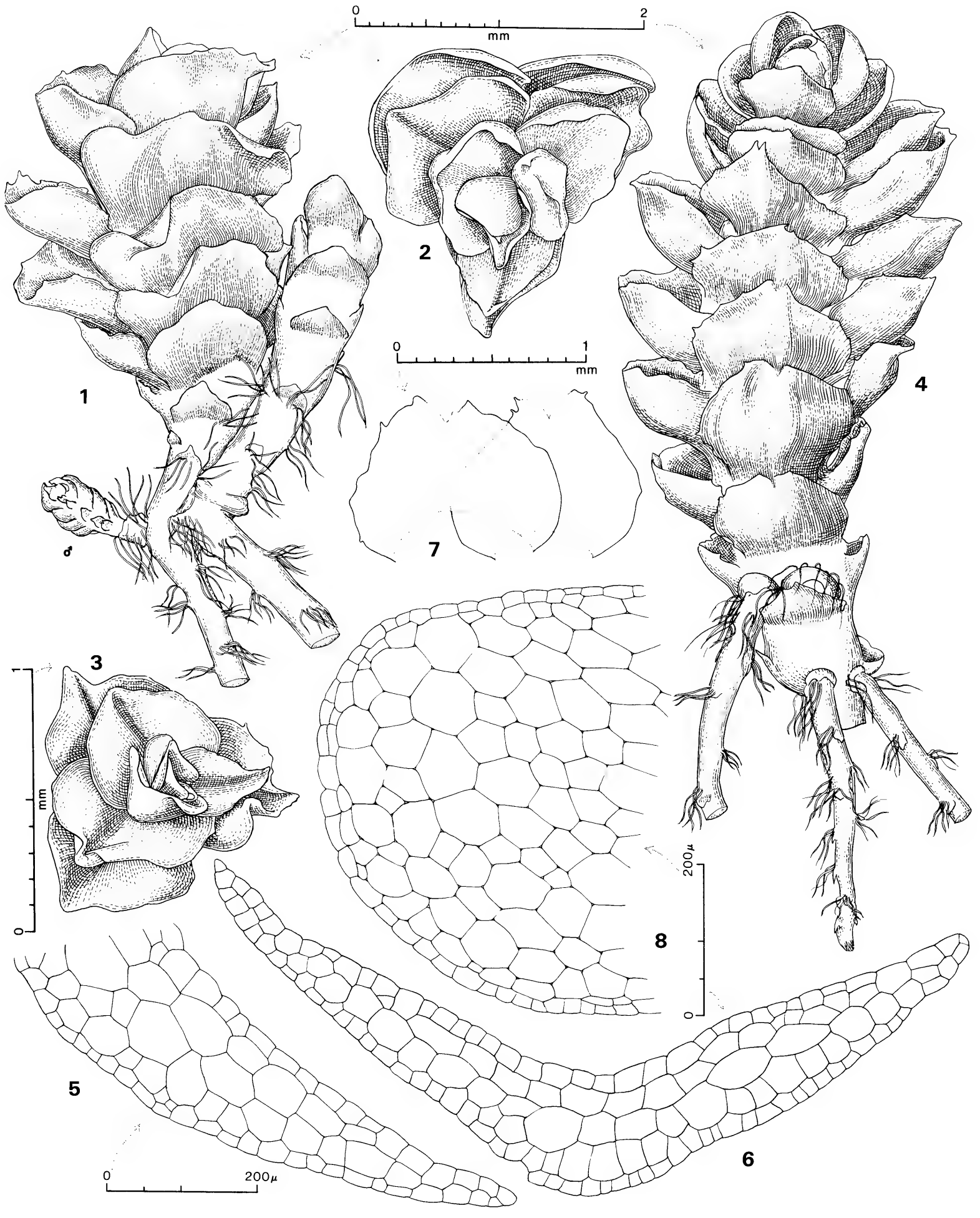

Fig. 114.
Hygrolembidium triquetrum J.J.Engel & R.M.Schust. 1. Leafy shoot with triradial, *Haplomitrium gibbsiae*-like facies; note androecial branch at left (= ♂). 2, 3. Views toward apex of shoot. 4. Leafy branch, ventral view; note 3 stoloniform branches and the collar of a fourth, severed branch. 5, 6. Leaves, cross sections through basal sector. 7. Underleaves, note that most of incision at apex is due to tearing (= stipple). 8. Stem, cross section through leafy shoot. (All from holotype.)

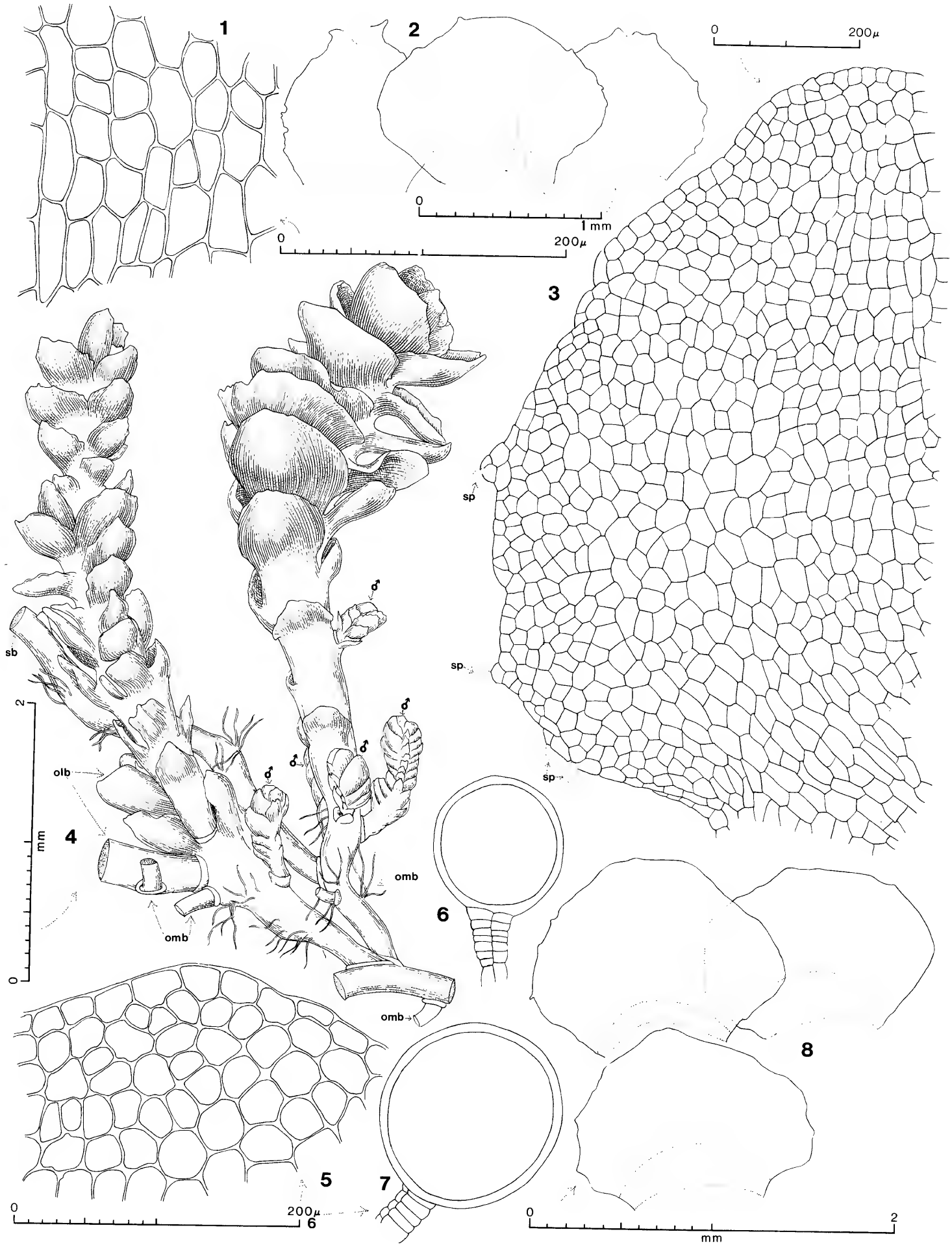

Fig. 115.
Hygrolembidium triquetrum J.J.Engel & R.M.Schust. 1. Median-basal leaf cells (outer face). 2. Two underleaves and, in middle, a leaf, all from same axis; note that most of incision at apex of underleaves is due to tearing (= stipple). 3. Sector of leaf (sp = slime papilla). 4. Portion of plant showing a smaller leafy branch at left, a stoloniform branch (= sb) and, at right, androecial branches from all 3 merophytes of a larger leafy branch (♂ = androecial branch; omb = old male branch, the distal portions withered and not shown; olb = old leafy branch). 5. Median-apical leaf cells. 6, 7. Antheridia, both at scale shown for fig. 7. 8. Leaves, all from one upright leafy shoot; upper and lower stippled lines for each leaf indicate adaxial and abaxial points of insertion respectively. (All from holotype.)

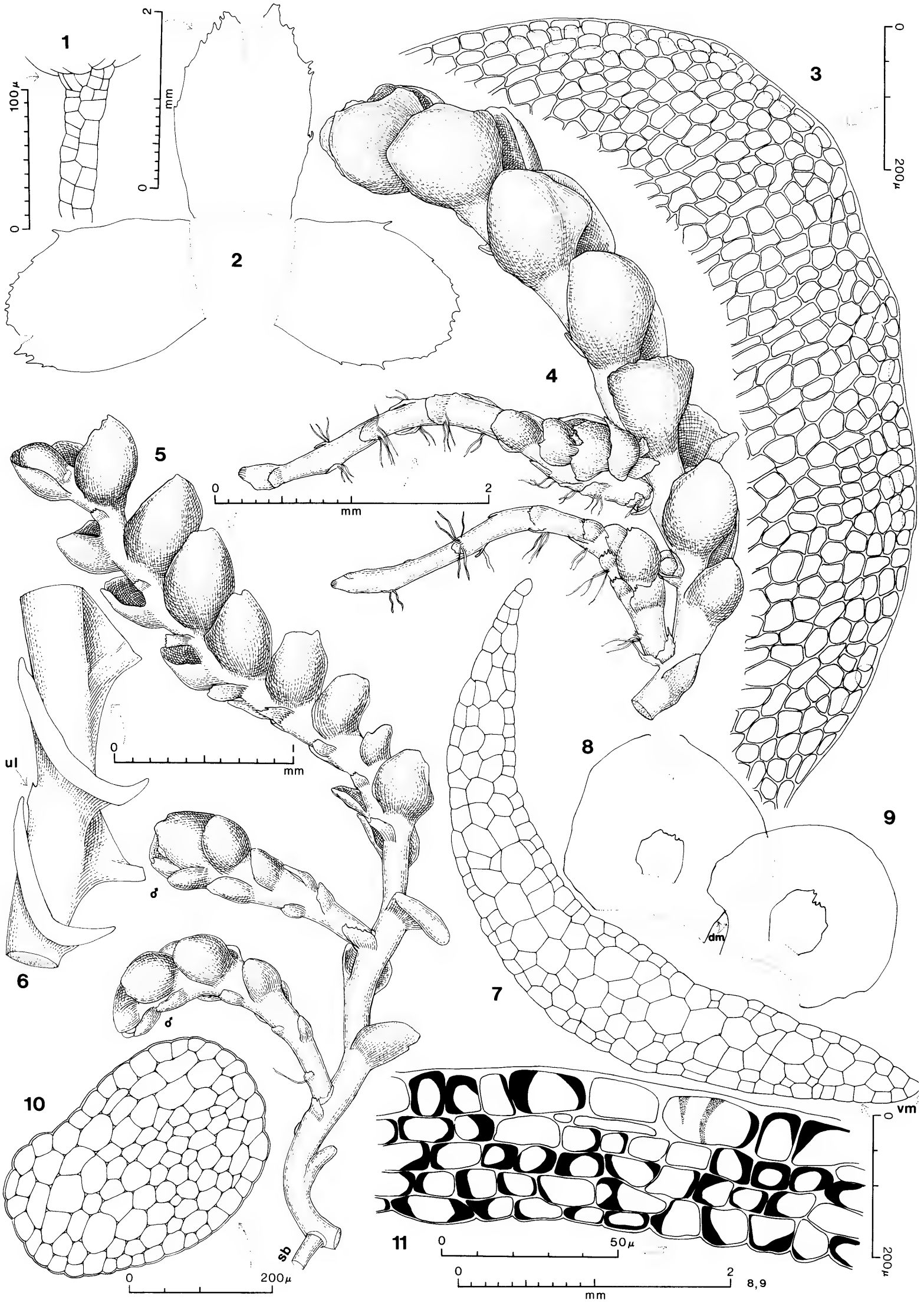

Fig. 116.
Hygrolembidium acrocladum (Berggr.) R.M.Schust. 1. Antheridium. 2. Bracts, and in middle, bracteole (note: figure drawn at 0.33× magnification of leaves and underleaves; note also triradial

Known from a few localities. At the Mt. Rocky summit area on Stewart Island plants occurred over soil protected by a rock ledge in mosaic communities of dense heath-forming shrubs to 3 m tall, herbs and dwarf heaths to 0.5 m tall, dominated by stunted *Leptospermum scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus*. The type occurred in a very compact, dense mat mixed with *Pachyschistochila* cf. *childii* on soil of an ice-scoured slope in the alpine zone. In the Young Ra. (Aspiring Natl. Park) it was found on peaty soil in snowmelt seepage in *Marsippospermum gracile* and *Poa colensoi* grassland with *Cephaloziella* sp., *Ditrichum difficile*, *Gaultheria novae-zelandiae* var. *depressa*, *Pachyschistochila subhyalina* and *Polytrichastrum alpinum*.

Comments: The subisophyllous to ± isophyllous, erect, triquetrous shoots are distinctive, even in the field (Fig. 114: 1–4). Leaves are fleshy and in basal cross section are 5–7-stratose, with the epidermal cells averaging smaller in diameter than the internal cells (Fig. 114: 5, 6). The cell width notably remains nearly the same from leaf apex to base, 21–32 μm (Fig. 115: 3). The species is closely allied to *Hygrolembidium rigidum* and the two are placed in a separate section of their own, sect. *Rigidae*.

Subg. ***Hygrolembidium***

Hygrolembidium acrocladum (Berggr.) R.M.Schust.

[Fig. 113: 4, oil-bodies, p. 504; Figs. 116, 117]

Aplozia acroclada Berggr., On New Zealand Hep. 9. *f. 8*. 1898. *Jungermannia acroclada* (Berggr.) Steph., Sp. Hepat. 2: 68. 1901. *Hygrolembidium acrocladum* (Berggr.) R.M.Schust., J. Hattori Bot. Lab. 26: 277. 1963. Lectotype (*fide* Grolle, 1966d): New Zealand, North Is., near Lake Taupo, 600 m, 1874, *Berggren 2874* (type not found in LD).

Aplozia lacerata Rodway, Tasman. Bryoph. 2: 32. 1916. Type: Tasmania, Mt. Wellington plateau, ?*Rodway* (MANCH!).

Lembidium isodictyon Herzog, Ark. Bot. N.S. 1: 488. *f. 6, 7*. 1952 (1951). *Hygrolembidium isodictyon* (Herzog) R.M.Schust., J. Hattori Bot. Lab. 26: 277. 1963. Lectotype (*fide* Grolle, 1966d): New Zealand, North Is., Plateau E of Waiotapu Valley, near Rotorua, *Allison H2170* (JE!).

Plants light green to light yellow-green, variable in size, the leafy shoots ranging from stoutly clavate, being only 650–750 μm wide and bearing 3–5 pairs of leaves to more robust, to 2.2 mm wide and bearing several to many pairs of leaves. Branching abundant, the leafy branches ventral- or lateral-intercalary and mostly from a system of creeping, freely branched, colorless, long slender stolons, the leafy branches rarely and sporadically issuing from leafy sectors of another leafy shoot and then only ventral-intercalary. Stem distinctly thick and fleshy for plant size, the cortex in 36–39 rows, leptodermous, poorly differentiated. Rhizoids

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symmetry; stipple distally indicates tear). 3. Distal portion of leaf. 4. Portion of main shoot with 2 ventral-intercalary androecial branches, lateral view; note ♂ branches proliferate vegetatively distally and become stoloniform. 5. Portion of main shoot with 2 ventral-intercalary androecial branches; note determinate ♂ branches (sb = stoloniform branch). 6. Sector of leafy shoot, lateral aspect, the leaves cut off except for basal ca. 0.25; note fleshy leaf bases (ul = underleaf). 7. Leaf, cross section through basal sector (vm = ventral margin). 8, 9. Leaves and within each, an underleaf, all from same upright leafy shoot (dm = dorsal margin). 10. Stem, cross section through leafy shoot. 11. Capsule wall, cross section. (All from *Engel 13950*, Tasmania, Cradle Mtn.)

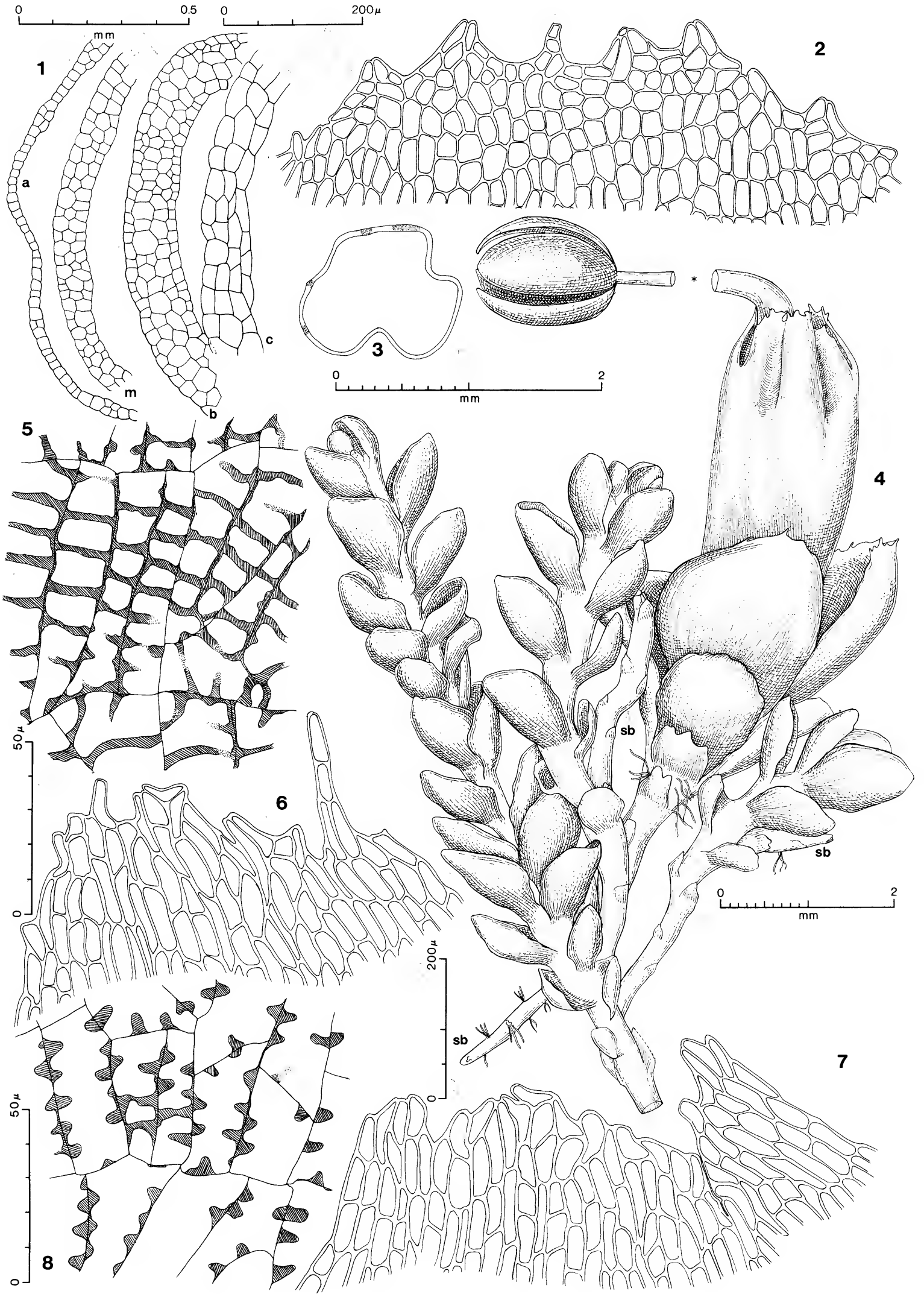

Fig. 117.
Hygrolembidium acrocladum (Berggr.) R.M.Schust. 1. Left to right: cross sections through 3 levels of perianth (a = distal 0.25; m = medium sector; b = base) and calyptra base (= c). 2. Distal portion of innermost bract. 3. Perianth, cross section through distal 0.25 (stippled areas indicate

mostly lacking on erect, leafy shoots, but if present, then from basal cells of underleaf or from stem at immediate base of underleaf. Leaves rather rigid, fleshy, polystratose in median and basal sectors, the median and distal sectors unistratose in an area below apex and within lateral margins; leaves in cross section toward base 3–5(6)-stratose in intramarginal sector, the marginal sector remaining polystratose or thinning to unistratose, the epidermal cells of leaf on average smaller in diameter than internal cells; leaves contiguous to closely imbricate, suberect to obliquely spreading, the insertion succubous in well-developed plants, ± transverse in smaller or weaker plants, the leaves deeply concave, at times subcupulate, orbicular (particularly in smaller plants) to suboblate, occasionally ovate, to 1120 μm wide × 1295 μm long when flattened; apex normally broadly rounded, less often truncate, sporadically repand, undivided, never retuse; lamina margins entire. Cells of apical sector subquadrate, at most short-rectangular, not elongate, the walls thin or slightly thickened, 22–36 μm wide × 22–45 μm long up to 35–40 μm wide × 35–50 μm long; median cells 24–32 μm wide × 32–56(62) μm long; basal cells 24–30 μm wide × 55–75 μm long; cells of unistratose region firm-walled, those of polystratose area leptodermous, delicate; surface smooth at least in median portion of leaf and often smooth throughout, distal cells occasionally faintly papillose, the marginal cells rarely so. Oil-bodies (in part after Schuster and Engel [1987b]) variable in number: 1–3 to 3–5, sometimes 6–9 per cell, coarsely and irregularly segmented and formed of a few variable, spherical segments; oil-bodies small, spherical and 4 μm in diam. to ovoid and 3–4.5 × 6–7(9) μm to 4–4.5 × 7–10 μm to broadly elliptic. Underleaves small, often inconspicuous and appearing as if lacking, the underleaves plane to weakly concave, wide-ovate to orbicular to suboblate, occasionally oblong or lingulate, the apex crenulate or with 1–3 teeth or irregular lobules; lamina margins entire or locally denticulate by projections of 1 or 2 cells.

Androecial branches originating from axils of underleaves, laxly spicate and at times subjulaceous; bracts erect, of similar form to leaves; antheridia 2–4 per bract, the stalk biseriate. Gynoecia on abbreviated ventral-intercalary branches, from lower, microphyllous sectors of leafy shoots; bracts and bracteoles concave, similar or bracteole somewhat narrower, the bracts considerably larger than leaves, ovate to wide-elliptic, the apex irregularly dentate or at times clearly 4-dentate-lobulate, the lamina margins with several teeth and (less often) ciliiform projections. Perianth very large for plant size, to 4.2 mm long × 1.4 mm in diam., subclavate to oblong-fusiform, cylindrical throughout or cylindrical below and faintly 3(4)-gonous above, the mouth crenulate to spinose dentate-lobulate; perianth 4–5-stratose at base.

Seta (*fide* Herzog, 1952) with 16–17 rows of outer cells. Capsule wall 4-stratose and 30–36 μm thick to 5-stratose and 42–46 μm thick; outer layer of cells equal to thickness of 1.8–3 of interior strata, the radial walls with nodular to spur-like thickenings on both longitudinal and most transverse walls, those of longitudinal walls sporadically extended tangentially to form complete, somewhat thickened semiannular bands; innermost layer of cells with radial walls often with ± continuous sheets of red-brown wall material, the radial walls also with rather thin semiannular bands and occasional nodular to spur-like thickenings.

Spores 15.8–17.8 μm in diam., the wall red-brown, with dense, low but sharply defined, close, papillose and short-vermiculate markings, 1.7–2.3× the elater diam. Elaters tortuous, bispiral, 7.2–9.6 μm in diam., the spirals 2.9–3.8 μm wide.

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bistratose sectors, the remainder unistratose). 4. Portion of plant with main leafy shoot, 2 ventral-intercalary leafy branches and a gynoecium with mature sporophyte; note isophyllous gynoecium (sb = stoloniform branch). 5. Capsule wall, inner layer. 6, 7. Portion of perianth mouth (each fig. from a different perianth). 8. Capsule wall, outer layer. (All from *Engel 13950*, Tasmania, Cradle Mtn.)

Distribution and Ecology: New Zealand: Stewart Island (600–690 m), South Island (560–1525 m), North Island (305–2000 m); Australia: Tasmania, Victoria, New South Wales. In New Zealand known from Fiordland (Hunter Mtns.), Otago (Pisa Ra., Old Man Ra., Maungatua, Swampy Summit, Lammermoor Ra., Rock and Pillar Ra.), Westland (Aspiring Natl. Park, Nelson Lakes Natl. Park), Canterbury (Harman Pass, Arthur's Pass, Porters Pass), Sounds–Nelson (Richmond Ra.), Southern North Island (Tararua and Ruahine ranges) and Volcanic Plateau (Kaimanawa Ra., Atiamuri, Rotorua) EPs.

A medium- to high-elevation species. In forested areas it occurs on well-shaded rocky cliffs, while in penalpine communities it may be found, for example, in and at the edges of peaty, saturated bogs or between boulders. On Stewart Island (Mt. Rakeahua summit area, 600–690 m) present over a thick soil layer in a pocket between boulders in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* 0.5–2 m tall and significant areas of exposed rock. Also at the summit area of Te Rangaakapua (Urewera Natl. Park, Huiarau Ra., 1265–1320 m) occurring on the floor in open areas and on small banks of soil in open areas within mosaics of stunted *Olearia colensoi* and tussock with occasional *Coprosma* spp. Below the summit of "Little Moehau" (Coromandel Forest Park, ca. 800 m) the species formed a pure colony on the exposed side of a seepage area in a mosaic of *Sphagnum* bog and small communities of shrub-heath including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus*, *Corokia*, and occasional stunted *Weinmannia silvicola* and *Dacrydium cupressinum*. In alpine communities it occurs over moist, peaty ground at edges of rills or tarns where it may form pure, compact colonies. Also over soil of protected pockets or of narrow crevices of boulders in areas of cliffs and outcrops with scattered alpine plants. The species often occurs as a pioneer over bare soil and the extensive, deep system of subterranean rhizoidous axes may be of significance in consolidating and stabilizing such habitats. In the bare soil niches often in pockets or under the lip of overhangs or under rock ledges, and, in such cases, at least a nominal amount of moisture and protection is provided. Also, in these niches *Hygrolembidium acrocladum* often is one of the few hepatics present. In wet peat-soil habitats it occurs with *Allisonia cockaynei*, *Kurzia compacta*, *Marchantia foliacea* and *Solenostoma inundatum*. In better-drained and bare soil sites it is found with *Chrysoblastella chilensis*, *Ditrichum cylindricarpum*, *Notoligotrichum australe* and *Polytrichum juniperinum*.

Comments: Similar to *Hygrolembidium rigidum* in the form of the leaf cells: non-elongated, chiefly 5–6-angled, with walls thin or at best very faintly firm-walled. Also approaching that species in the densely imbricate leaves, the shoots becoming stoutly julaceous and in its translucent light green to green color. Plants are at once distinct from *H. rigidum* in: 1) leaf cells much the same in size throughout the leaf; 2) leaf cells all (at least the epidermal) with 1–2 small, coarsely botryoidal oil-bodies; 3) surface of the leaves quite smooth, even distally; 4) leaves more nearly orbicular, never folded above; and 5) underleaves all small and appressed, the shoots never trigonous as seen in apical profile.

The underleaves although small are normally quite visible (Fig. 116: 5), but are sometimes inconspicuous and then appear as if altogether lacking. Shoots frequently have a mixture of conspicuous and inconspicuous underleaves. However, occasional shoots have underleaves uniformly reduced and thus, at first glance, appear underleaf-free.

Small phases of this species sometimes may be mistaken for *Solenostoma totipapillosum*, but the presence of underleaves and the lack of papillae on the stem will immediately distinguish *Hygrolembidium acrocladum* from that species.

Hygrolembidium australe (Steph.) Grolle

[Plate 11C]

Hygrobiella australis Steph., Sp. Hepat. 3: 358. 1908. *Metahygrobiella australis* (Steph.) R.M.Schust., Bryologist 64: 206. 1961. *Lembidium australe* (Steph.) Grolle, J. Hattori Bot. Lab. 26: 4. 1963. *Hygrolembidium australe* (Steph.) Grolle, J. Jap. Bot. 41: 229. 1966. Type: New Zealand, South Is., Arthur's Pass, *Goebel* (G!).

Lembidium stereophyllum Herzog, Ark. Bot. N.S. 1: 491. *f. 8–9.* 1952 (1951). *Hygrolembidium stereophyllum* (Herzog) R.M.Schust., J. Hattori Bot. Lab. 26: 277. 1963. Type: New Zealand, North Is., Tararua Mtns., Mt. Hector, Watercourse W of Kime Hut, ca. 4200 ft., 31 Dec. 1933, *Zotov* (CHR ex herb. Hodgson no. 39!).

Plants pure, clear green, variable, especially in size, the leafy shoots to 1.5 mm wide. Branching abundant, the leafy branches ventral- or lateral-intercalary and from a system of creeping, freely branched, colorless, long, slender stolons, the leafy branches issuing only from microphyllous sectors of plants and not from leafy sectors of another leafy shoot. Stem cortical cells leptodermous, usually in 19–20 to over 30 rows, the medullary cells very large, pellucid. Rhizoids mostly lacking on erect, leafy shoots, but if present, then from basal cells of underleaf or from stem at immediate base of underleaf. Leaves rather rigid, fleshy, polystratose in median and basal sectors, the peripheral and distal sectors unistratose in an area below apex and within lateral margins; leaves in cross section toward base 3–5-stratose in intramarginal sectors, the marginal sectors remaining polystratose or thinning to unistratose; epidermal cells of leaf moderately smaller in diameter than internal cells; leaves increasing in size upward, or (on longer shoots) remaining ± equal in size except for smaller leaves near the apex, the leaves contiguous to moderately imbricate, suberect to obliquely spreading, ± loosely sheathing stem, feebly to distinctly succubously inserted, deeply concave, at times subcupulate, ovate, widest in basal one third or in the middle and narrowed to the blunt, very concave, undivided, never retuse apex; lamina margins entire. Larger leaves (700)950–1100 μm wide × (1000)1120–1200 μm long (when flattened, which is difficult to do without tearing the leaf). Cells of apical sector ± strongly elongated, narrowly oblong, ± prosenchymatous, thick-walled, (12)15–26 μm wide × (35)40–60(90) μm long; median cells 18–26 μm wide × 34–50(72) μm long; basal cells not or hardly larger; cells of unistratose region firm-walled, those of polystratose area leptodermous, delicate, chlorophyllose; surface of distal and marginal cells papillose (sometimes faintly so), that of median portion of leaf smooth or (rarely) delicately granulate-papillate. Oil-bodies (Schuster and Engel, 1987b) lacking in unistratose portion of leaf, present in all or most cells of polystratose region, there 1–2(3) per cell (some internal cells with 3–9 oil-bodies); oil-bodies small, glistening, 2.5–3.5 × 5 μm to 3.5–5 × 5–6 μm, the smaller sometimes unsegmented, the larger coarse, few-segmented. Underleaves small, often inconspicuous and appearing as if lacking, plane to weakly concave, variable in shape: lingulate to oblong-ovate or wide-ovate to suborbicular, the apex crenulate; lamina margins entire. Fungal partner an ascomycete.

♂ Plants small. Androecial branches originating from axils of underleaves or leaves, sometimes very small and slender, at other times a little less vigorous than smaller vegetative branches; bracts unlobed, of similar form to leaves, the apices and sides suberect; antheridia (1)2–3(4) per bract, the stalk 2–4-seriate. Gynoecia on ± abbreviated ventral- or lateral-intercalary branches; bracts and bracteoles concave, similar or bracteole somewhat smaller, the bracts widely spaced, somewhat larger than leaves, ovate to wide-elliptic, the apex 0.15–0.2(0.4) bilobed and with lobes variable-denticulate above (often with free ends of elongated

cells ± sigmoid) or unlobed and blunt to broad-acute, crenulate, the lamina margins entire or with a ciliiform projection. Perianth very large for plant size, to 3 mm long × 1.4 mm in diam., oblong-fusiform or (less often) ovate, cylindrical below and bluntly 3(4)-gonous above, the mouth lobulate-fimbriolate to crenulate-ciliolate with narrow, often strongly elongated cells and short cilia (to 120 μm long); perianth 3–4(5)-stratose in basal and median sectors.

Seta with (14)16–18 rows of large epidermal cells. Capsule ellipsoidal, the wall 3–4(5)-stratose and ca. 35–39 μm when 5-stratose; outer layer of cells with 2–3 to 4–6 nodular thickenings per face of all or almost all longitudinal walls (primary walls sometimes with thickenings weaker and more yellowish, rather than brownish); innermost layer of cells with almost exclusively nodular to weak or imperfect semiannular thickenings.

Spores 13.5–17.5 μm in diam., the wall yellow-brown, papillate-granulate to papillate, the markings partly coalescent and forming short-vermiculate lines, the spores 2× the elater diam. Elaters ± tortuous, bispiral, 6.7–9.5 μm in diam., the spirals 3–3.3 μm wide.

Distribution and Ecology: Endemic to New Zealand: Campbell Island, South Island (1000–1550 m), North Island (840–1800 m). Known from Fiordland, Southland (Blue Mtns.), Otago (Rock and Pillar Ra.), Westland (Spenser Mtns., Mt. Te Kinga, upper Otira River), Western Nelson (Mt. Peel), Sounds–Nelson (Richmond Ra.) and Auckland (Mt. Moehau) EPs.

Widespread but sporadic in distribution. The species occurs primarily in alpine and penalpine, moory sites mostly at 855–1800 m, but sporadically at lower elevations (520–825 m). In the alpine zone it grows along small rills in deep shade under tussock blades where conditions are permanently moist. Also over soil near the edges of tarns and on lips of stagnant pools in mosaics of tussock grass and alpine vegetation along with tarns, pools, rills, rocky outcrops and boulderfields. In these sites it grows with *Sphagnum cristatum*, *S. falcatulum* (growing at times on the surface of the *Sphagnum*), *Campylopus clavatus*, *C. introflexus*, *Kurzia hippuroides* and *K. calcarata*, *Pachyglossa tenacifolia*, *Pseudocephalozia paludicola* and *Siphula rubra*. The species also may be found in more exposed situations; for example, it occurs over bare soil of exposed portions of slopes as well as over soil of pockets on ice-scoured slopes. In penalpine communities the species occurs over soil in vegetation dominated by *Chionochloa* (but with some scattered *Dracophyllum* and *Phormium cookianum*) as well as near rills or under tussock overhangs in scrub consisting mainly of *Chionochloa*, *Dracophyllum* and *Hebe*. In these sites it occurs with *Cladia aggregata*, *Conostomum pusillum*, *Ditrichum difficile*, *D. punctulatum*, *Notoligotrichum australe*, *Philonotis tenuis* and *Racomitrium lanuginosum*. At somewhat lower elevations over soil of vertical banks of drainage channels; e.g., on Mt. Moehau (Coromandel Forest Park, ca. 840 m) it occurred in a narrow truncated valley system under stunted *Weinmannia silvicola*, *Coprosma foetidissima* and *Corokia buddleioides*. The species rarely occurs in *Nothofagus* forests; e.g., near the South Branch of Borland Burn (Fiordland, 855–870 m) the species occurs over peaty soil at the side of a normally dry stream channel.

Comments: Vegetatively this species, like other *Hygrolembidium* species, is extremely variable, especially in size. Plants often are dwarfed and bear smaller, often shorter, less concave leaves, never folded at the tips; they seem always to be rather remote-leaved.

All forms of *Hygrolembidium australe* are at once distinct from *H. rigidum*, which may occur admixed with this species, in the 1) bluntly pointed to ± rounded leaves whose apices are never incised or retuse; 2) much smaller underleaves; and 3) firm-walled leaf cells (except at the leaf bases), strongly elongated and (marginally) prosenchymatous in form. Also, oil-bodies are present at least in some cells; in *H. rigidum* no cells ever bear oil-bodies.

Chloranthelia R.M.Schust.

Chloranthelia R.M.Schust., Nova Hedwigia 8: 278. 1964; J. Hattori Bot. Lab. 26: 215, 275. 1963, *nom. inval.*

Maculia E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 72. 1965.

Plants anisophyllous, erect or prostrate, greyish to pure green (without ability to develop secondary pigmentation), dull-textured and water-repellent when dry; leafy shoots small, the apices never with autonomous curvature. Branching normally all axillary and intercalary, from axils of both leaves and/or underleaves, the leafy branches ascending to erect, arising from and/or freely giving rise to geotropic, pale, leafless rhizomes or stolons which freely bear rhizoids, the leafy shoots usually unbranched, very rarely and sporadically producing a terminal, *Frullania*-type branch. Stem soft, with or without a hyalodermis; cortex with large, pellucid cells that are equal in size to or larger than the very leptodermous medullary cells; cortical cells in surface view oblong, lying in sharply defined tiers, superior in size to leaf cells. Rhizoids sparsely developed on leafy shoots, but if present, then toward shoot bases. Leaves adaxially concave or concave-canaliculate, but never canaliculate-conduplicate, unistratose, soft-textured, chlorophyllose except sometimes for marginal and submarginal cells, which are at times ± thicker-walled and hyaline, the insertion transverse to very weakly succubous; mature leaves variable, asymmetrically lobed, either 2(3)- or 3–4(5)-lobed for less than 0.35 their length; margins entire or denticulate-dentate. Cells non-collenchymatous, rather large, but an area basalis or apicalis not differentiated, in median and basal sectors ± oblong, the marginal cells typically echlorophyllose; surface clearly papillose. Oil-bodies completely lacking, only a few scattered, tiny, glistening oil-droplets present. Chloroplasts numerous, small: 1.4–2.4 × 2.4–4.3 μm. Underleaves distinct, 0.1–0.65× area of lateral leaves, erect-appressed and often nearly hiding stem, present throughout, the apex variable, 2–4-dentate or -lobulate; lamina margins as on leaves. Asexual reproduction lacking.

Dioecious. Androecia (known only for *Chloranthelia denticulata*) at base of abbreviated branches that may proliferate distally, lateral- or ventral-intercalary, spicate; bracts leaf-like, slightly smaller than leaves; antheridia 1 per bract, the stalk biseriate. Gynoecia arising on short, abbreviated, intercalary branches bearing at most 1–2 cycles of minute leaves, the branches either from axils of lateral leaves, or from axils of underleaves; bracts small, hyaline, leptodermous, suberect. Perianth mouth lobulate-incised, fimbriolate with long, linear cells distally.

Seta with 8 rows of outer cells surrounding 7–8 rows of smaller internal cells.

Spore wall asperulate. Elaters bispiral.

Type: *Chloranthelia denticulata* (Steph.) R.M.Schust. (≡ *Lembidium denticulatum* Steph.)

The genus includes two species, *Chloranthelia denticulata* (Steph.) R.M.Schust. of New Caledonia and *C. berggrenii* of New Zealand.

References: Schuster and Engel (1987b; mon.); Schuster (2000a).

Chloranthelia berggrenii (Herzog) R.M.Schust.

[Plate 10D–F]

Lembidium berggrenii Herzog, Ark. Bot. N.S. 1: 485. *f. 3 a–e*. 1952 (1951). *Chloranthelia berggrenii* (Herzog) R.M.Schust., J. Hattori Bot. Lab. 26: 266. 1963, *nom. inval. Chloranthelia berggrenii* (Herzog) R.M.Schust., Nova Hedwigia 10: 23. 1965. *Maculia berggrenii* (Herzog) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 73. 1965. Type: New Zealand, North Is., Papakauri, *Berggren 3269*.

Maculia filosa E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 72. 1965. *Chloranthelia filosa* (E.A.Hodgs.) R.M.Schust., Nova Hedwigia 15: 469. 1968. Type: New Zealand, South Is., Arthur's Pass area, Bealey River, Feb. 1874, *Berggren s.n.* (MPN 8446, herb. Hodgson no. 8446, *non vidi*); isotype: (CHR ex herb. Hodgson!).

Plants slightly greyish green when living, dull green in herb., rather opaque; leafy shoots to 1–1.15 mm wide, normally with numerous pairs of leaves, ± dorsiventrally complanate, arising from microphyllous, fleshy, subterranean axes, with erect, non-cernuous apices that are often slightly narrowed, the leafy shoots often with a rather lengthy basal, fleshy, microphyllous sector. Branching common, normally all intercalary, usually ventral, rarely isolated ones lateral; *Frullania*-type branches exceedingly rare; stolons geotropic, frequent, ventral-intercalary. Stem rather pellucid, soft textured, thick and fleshy for plant size, the cortex poorly differentiated, with cells pellucid, rather thin-walled, large (cortical cells averaging much larger than leaf cells), in surface view lying in few, irregular tiers between successive leaves; medullary cells even more hyaline, as large as to somewhat larger in diameter than cortical cells. Rhizoids sparsely developed on leafy shoots, sometimes present at underleaf bases in basal, microphyllous sector. Leaves contiguous to loosely imbricate, widely spreading, very concave, weakly succubously inserted, broadly and rather asymmetrically ovate, not at all keeled, from 545–625 μm wide × 630–760 μm long (then ca. 1.2–1.3× as long as wide) to, on robust shoots, 705–750 μm wide × 610–625 μm long (then 1.1–1.2× as wide as long), asymmetrically 3–4(5)-lobed or lobulate, the deepest sinuses descending to 0.15–0.25(0.35); ventral 1–2 lobes clearly longer, the larger ones 7–8 cells wide at base, the dorsal (1)2 lobes smaller, shorter, the dorsal-most only 0.55–0.75 length of ventral lobes, *in situ* often appearing like a tooth on dorsal leaf margin; lobes triangular, the dorsal often sharp, the others mostly blunt to bluntish, mostly weakly to strongly incurved; lobes in suboptimal plants narrower and lanceolate to acute-acuminate, the ventral ones being only 3–5 cells wide at base; lamina margins not hyaline, entire, repand, or 1 or both margins occasionally with 1–3 small teeth toward the base. Cells of leaves leptodermous throughout, delicate, lacking all trace of trigones, small in apices and lobes, there 23–28(30) × (23)25–32 μm, toward base gradually much larger, becoming 40–52 μm wide × 65–80 μm long; surface conspicuously papillose (toward leaf bases inconspicuously striolate). Oil-bodies completely lacking, only a few scattered, tiny, glistening oil-droplets present. Chloroplasts numerous, small: 1.4–2.4 × 2.4–4.3 μm. Underleaves ca. 0.15–0.3 the size of adjacent lateral leaves, not or scarcely as wide as stem (*in situ*), loosely appressed to moderately patent from stem, distant to feebly imbricate above, ovate to rotund-quadrate; apices 3–4-lobulate or -dentate, weakly concave, not keeled, the lobes often consisting of 1 or 2 linear cells or lobes larger and terminating in a uniseriate row of 2 linear cells, the apical cell often with ephemeral terminal slime papilla; lamina margins entire or crenulate-denticulate or denticulate. Fungal partner absent.

Androecia unknown. Gynoecia (only immature ♀ seen) produced in great abundance on very abbreviated weak ventral-intercalary (rarely isolated ones lateral-intercalary) branches

originating in a broad zone extending from the basal microphyllous sector well into the zone with normal leaves, not restricted to shoot bases; gynoecial branches bearing 1–2 cycles of minute leaves, then the hyaline, small, leptodermous, suberect cycle of bracts + bracteole.

Distribution and Ecology: Endemic to New Zealand: South Island (200–1320 m), North Island. Known from Fiordland, Otago, Westland, Canterbury and Northland EPs.

Known from a small number of widely scattered sites. In the South Island known from Wet Jacket Arm (Fiordland), Morrisons Burn (Dunedin), Mt. French (Hohonu Ra., Westland), Governors Bush (Mt. Cook Natl. Park, 760 m), Temple Basin and Bealey River (Arthur's Pass area, type locality of *Maculia filosa*) and Mole Saddle (Ella Ra., N of Lewis Pass). In the North Island occurring at Papakauri (probably near Bay of Islands; see Schuster and Engel, 1987b, p. 334). The Morrisons Burn plant is from a roadside bank, under *Blechnum*, associated with *Lembidium nutans*, at the edge of a forest of *Aristotelia serrata*, *Griselinia littoralis*, *Fuchsia excorticata* and *Pittosporum eugenioides*. At Wet Jacket Arm the plants occurred under *Nothofagus menziesii* forest, on soil with *Diplophyllum dioicum*, *Pachyschistochila colensoana* and *Bartramia papillata*. At Temple Basin the plants grow under overhanging soil banks in *Dracophyllum rosmarinifolium – Podocarpus nivalis* scrub. The Governors Bush plants occurred on bare earth on a damp bank under an overhang in tall penalpine scrub. On Mt. French the plants were on a vertical soil bank in *Olearia colensoi – Dracophyllum longifolium – Chionochloa flavescens* scrub on a bluff and were growing with *Pleuridium arnoldii*, *Isotachis montana* and *Jensenia connivens*. *Lembidium nutans* and *Chloranthelia berggrenii* agree in their basic ecology: both appear confined to fine-grained, loamy, water-retentive soil.

Comments: The growth habit of this species is closer to that of *Lembidium nutans* than to that of *Chloranthelia denticulata*, the type of *Chloranthelia*. Underleaf form (especially the form of the minute lobes), stem anatomy and the great disparity between the hyaline, very large cortical cells and the small dense upper leaf cells all suggest a close affinity to *L. nutans*. The closely papillose distal portions of the leaves and almost smooth, large-celled leaf bases are also as in that species. However, the essentially constant intercalary branching, and the more clearly and asymmetrically lobed leaves suggest a closer affinity to *C. denticulata*. Final placement of this species must await discovery of androecia and sporophytes. The species differs from all New Zealand taxa in the succubous, strongly asymmetrically 4-lobed leaves with reduced dorsal lobes.

Subfam. ***Megalembidioideae*** J.J.Engel

Subfamily *Megalembidioideae* J.J.Engel *in* J.J.Engel & Braggins, J. Hattori Bot. Lab. 97: 88. 2005.

Megalembidium R.M.Schust.

Megalembidium R.M.Schust., J. Hattori Bot. Lab. 26: 258. 1963. *Kurzia* sect. *Megalembidium* (R.M.Schust.) Grolle, J. Jap. Bot. 39(3): 80. 1964.

Plants dendroid, the main erect shoots and branches isophyllous or nearly so, the plants pale green to pure green, the lower sectors of main axis brownish with age, medium-sized, the leafy axes to 3.5 cm high. Plants with a strongly developed system of basal, creeping, plagiotropic rhizomes, from which arise erect, leafy shoots that distally are copiously and 2–3-pinnately

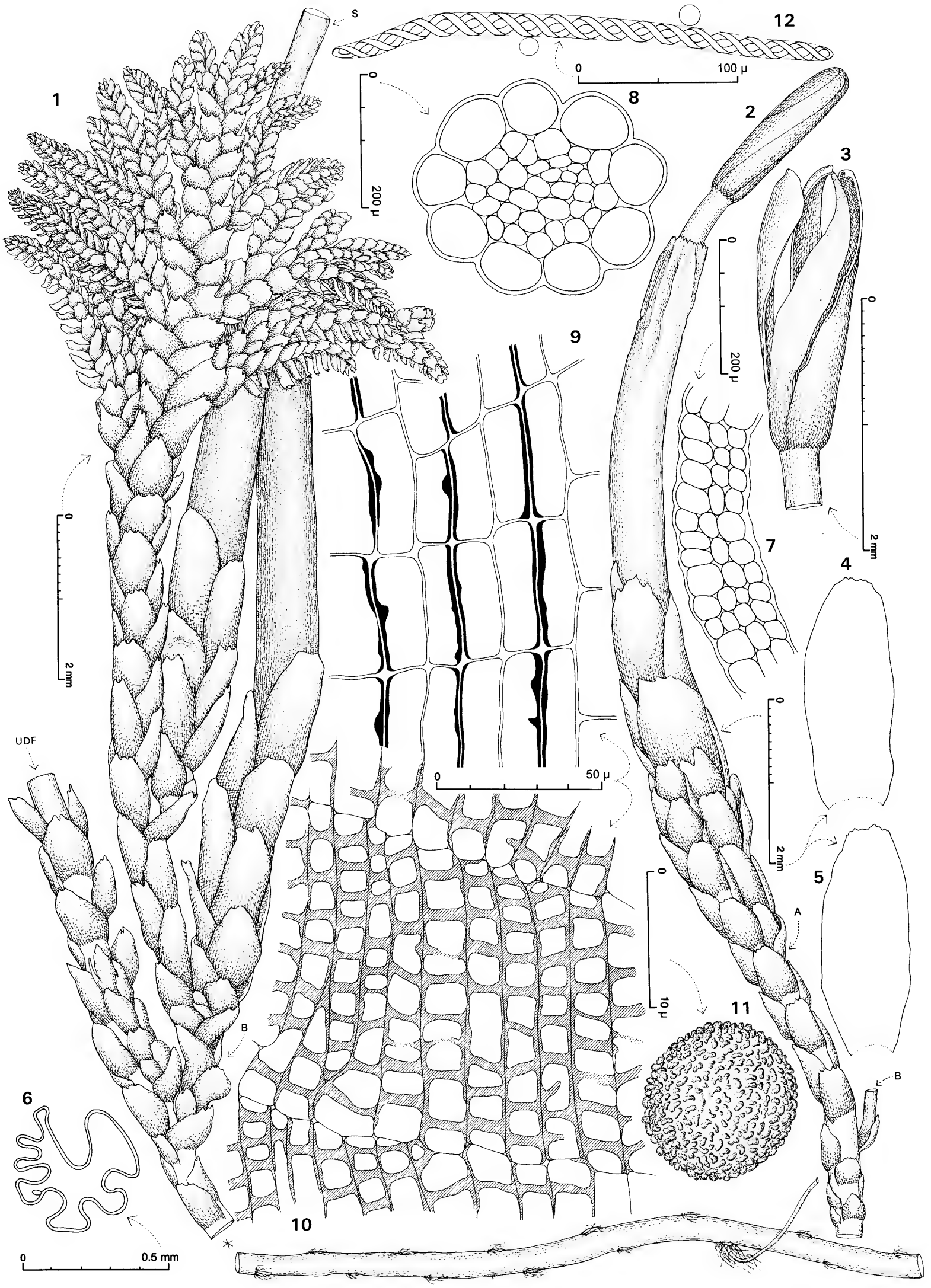

Fig. 118.
Megalembidium insulanum (W.Martin & E.A.Hodgs.) R.M.Schust. 1. Plant showing an erect, pinnately branched, dendroid "frond," 2 perianths (one with a mature sporophyte = S) and, at base, a stolon, dorsal view, the stolon has an intercalary origin from extreme base of leafy shoot (basal to

branched; rhizome and leafless sectors of erect axes giving rise to intercalary, geotropic, microphyllous, root-like axes, which in turn give rise to intercalary, considerably more slender secondary branches ("secondary roots"). Branches of erect shoot system crowded distally, regular, determinate in length, on one side of axis of *Frullania* type, on the opposite side of *Microlepidozia* type, the ultimate branches often weakly cernuous or circinate, the erect shoots unbranched below. Stems of primary aerial axes rigid, comprised of a hyaloderm of numerous, slightly thick-walled, hyaline or pigmented cortical cells that collapse with age and (1)2–3 subepidermal layers of small, fuscous, strongly thick-walled cells, grading into a medulla of ± thin-walled colorless cells. Leaves unistratose, those of main aerial axes basal to onset of branches erect, appressed to stem, ensheathing and hiding much or all of the stem, fragile, hyaline, incubously inserted, deeply concave-cucullate, 650–750 μm wide × 620–680 μm long, ovate, the apices narrow, (3)4-dentate-lobulate to 0.1; lobes terminating in a single cell or a uniseriate row of 2(3) cells, the lobe cells ± uniform in size and with at most small trigones. Leaves of main aerial axes distal to onset of branches not sheathing the stem, obliquely spreading, more deeply lobed than the leaves below, the lobe cells differentiated: those of uniseriate row and cells immediately below conspicuously larger than those toward lobe base, the latter with bulging trigones. Primary branch leaves smaller, concave, broadly ovate and more broad-based than those of main aerial axis, the apices 3–4-lobulate. Secondary branch leaves smaller than those of primary branches, the apex 2–3-dentate-lobulate. Tertiary branch leaves smaller than those of secondary branches, the apex short-bifid. Cells in median sector of main aerial axes leaves basal to onset of branches somewhat elongated, ± thin-walled, with minute trigones; cells in median sector of main aerial axes leaves distal to onset of branches subisodiametric or at most slightly elongated, firm-walled, with distinct trigones; surface striate-papillose. Oil-bodies totally absent. Underleaves similar to leaves of same shoot-sector except a little smaller and occasionally with one tooth fewer, the underleaves of ultimate branches bidentate-lobulate. Asexual reproduction lacking. Fungal partner an ascomycete.

Dioecious. Androecia on short, abbreviated, ventral- and lateral-intercalary branches from leafless bases of main aerial axes, the androecia spicate, whitish, variable, sometimes appearing to cease growth and then compact and bud-like to vermiform, but at other times proliferating vegetatively with the production of several small, sterile, scale-like leaves prior to the formation of a new androecium; bracts strongly ventricose-cucullate, the apex retuse to bidentate; antheridia usually 1 (at times 2) per bract, the stalk variable, uniseriate throughout or locally with 1 or a few biseriate tiers; bracteoles lacking antheridia. Gynoecia on reduced, highly abbreviated ventral-intercalary branches, the gynoecia strongly dorsally assurgent and becoming parallel or nearly so with upright leafy shoots, slender throughout and not swollen and rhizoidous at base; bracts in 4 series that all closely ensheath the gynoecium (including the mature perianth), the bracts concave, appearing membranous and like onionskin, those of second

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point at B, at arrow); not shown at point B are 4 additional gyres of leaves; several other stolons also originate from near the point of origin of the stolon shown, resulting in a basal system of stoloniform axes; the other upright, dendritic "frond" (at position indicated by UDF) not shown. 2. Portion with 2 sporophyte-bearing gynoecia, one originating at point A, the other (not shown) at point B; also shown at left is basal portion of leafy branch; note the spiral lines of dehiscence. 3. Capsule showing spirally twisted valves. 4, 5. Innermost ♀ bracts. 6. Distal portion of perianth, cross section. 7. Perianth base, cross section. 8. Seta, cross section. 9. Capsule wall, outer layer. 10. Capsule wall, inner layer. 11. Spore. 12. Elater and outline of 2 spores. (All from *Braggins 98474C*, New Zealand, Westland Natl. Park, Omoeroa Saddle.)

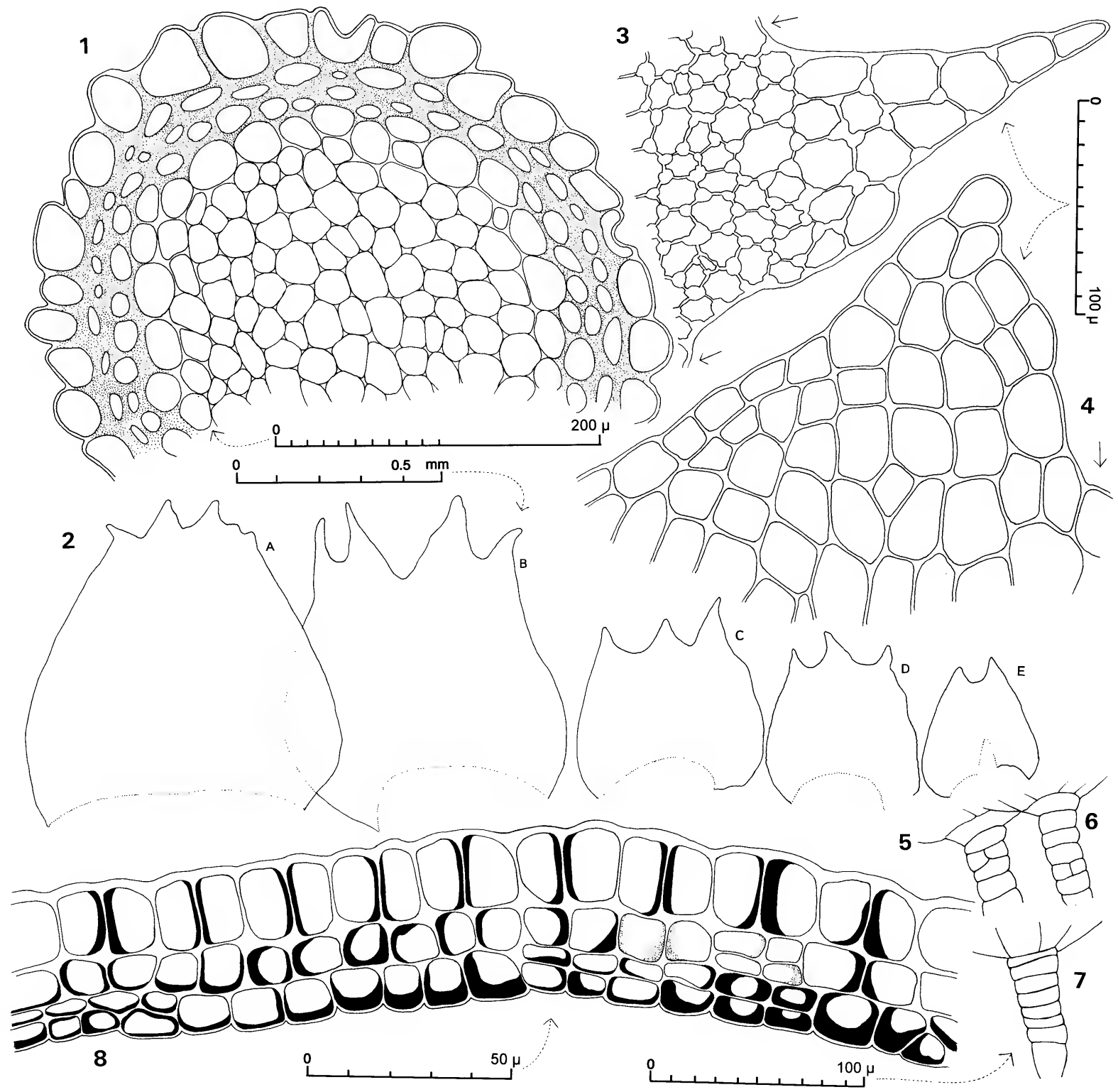

Fig. 119.
Megalembidium insulanum (W.Martin & E.A.Hodgs.) R.M.Schust. 1. Stem, cross section. 2. Leaves (left to right and all drawn to same scale): A = leaf of main shoot below level of onset of branches; B = leaf of main shoot above level of branches; C–E = leaves of primary, secondary and tertiary branches, respectively. 3. Lobe of main shoot leaf above level of branches, arrows indicate sinus bases (note enlarged cells). 4. Lobe of main shoot leaf below level of branches (note undifferentiated cells). 5–7. Antheridial stalks. 8. Capsule wall, cross section. (Figs. 1–4, 8, from *Braggins 98474C*, New Zealand, Westland Natl. Park, Omoeroa Saddle; 5–7, from *Engel 24675*, New Zealand, Stewart Is., Pryse Peak.)

and third series (from base) often narrowed toward a 2–3-lobulate apex, the gynoecium also with a few scale-like bractlets at base; bracts and bracteole of innermost series identical or nearly so, firmly attached, erect, mutually connivent, together tube-like and tightly ensheathing the lower sector of the perianth, deeply concave-canaliculate, long-elliptic-sublinear, the apices broadly rounded, the apical and subapical cells thin-walled and distinctly striate-papillose, the apex with 4 rounded projections (lobules) barely perceptible; lamina cells di-

morphic, those of a broad median field ± rectangular, with walls strongly thickened and red-brown, the surface striolate, those of margin and submargin irregular in shape, with walls thin and pale yellow-brown, the surface smooth or faintly striate-papillose, the marginal cells variable in shape, often long and narrow, the apical or free end of marginal cells often divergent and forming a crenulation, the margins otherwise with a few slime papillae. Perianth long-emergent, markedly slender and elongate-fusiform (to 9× longer than wide), terete in basal and median sectors, the distal sector obscurely trigonous, pluriplicate, the perianth strongly narrowed, contracted and ± pointed toward the apex; mouth shallowly lobulate, the cells thin-walled, rather elongated, laterally free for typically less than 0.5 the cell length but typically free for only very short distances, the mouth thus crenulate-denticulate, the cells at the mouth and those immediately below mouth distinctly striate-papillose; perianth 3(locally 4)-stratose in basal portion.

Seta with 9 rows of very large, firm-walled, outer cells (each with their free face bulging), surrounding an inner core of 28–32 much smaller cells. Capsule long-linear, with spiral dehiscence, the valves spirally twisted, long-linear and strap-shaped, the wall 38–46 μm thick, of 3–4 (locally 5) layers, the outer layer subequal to the combined inner layers, or slightly less thick, the exposed wall firm; outer layer of cells in tiers, rather regularly rectangular, with two-phase development, the longitudinal walls with well-defined, weakly sinuous, sheet-like thickenings and, sporadically, a few ill-defined nodule-like thickenings alternating with walls that are devoid of thickenings, the transverse walls devoid of thickenings; intermediate layer(s) in cross section thickened in the corners; innermost layer of cells ± tiered, rather regularly, narrowly and markedly long-rectangular; semiannular bands common, rather close, usually complete.

Spores 11.5–14.4 μm in diam., pale yellow-brown, with rather close granular-finely papillose markings and short vermiculae; spore:elater diam. ratio 1–1.2:1. Elaters rigid, many nearly perfectly straight, 10.6–12.5 μm wide, bispiral to tips, the spirals closely wound, notably wide, 4.8–6.2 μm wide.

Type: *Megalembidium insulanum* (W.Martin & E.A.Hodgs.) R.M.Schust. (≡ *Lembidium insulanum* W.Martin & E.A.Hodgs.)

The genus is monotypic.

References: Engel and Braggins (2005); Herzog (1951 *sub Dendrolembidium*); Schuster (1963b, 1980a, 2000a).

Megalembidium insulanum (W.Martin & E.A.Hodgs.) R.M.Schust.

[Plate 11A, B; Figs. 118–120]

Lembidium insulanum W.Martin & E.A.Hodgs. *in* W.Martin, Trans. & Proc. Roy. Soc. New Zealand 78: 497. 1950. *Dendrolembidium insulanum* (W.Martin & E.A.Hodgs.) Allison & E.A.Hodgs. *in* Allison, Trans. Roy. Soc. New Zealand 88: 11. 1960. *Megalembidium insulanum* (W.Martin & E.A.Hodgs.) R.M.Schust., J. Hattori Bot. Lab. 26: 258. 1963. *Kurzia insulana* (W.Martin & E.A.Hodgs.) Grolle, Rev. Bryol. Lichénol. 32: 175. 1964 (1963). Type: New Zealand, Stewart Is., Pegasus Creek, near waterfall, 9 Jan. 1949, *Martin 568* (CHR – *absens*).

Dendrolembidium martinii Herzog, Ark. Bot. II. 1: 500. *f. 12, 13: a–e*. 1951. Type: New Zealand, Stewart Is., Table Hill, 5 Feb. 1947, *Martin* (CHR – *absens*).

The generic description serves to characterize the single species.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (3–690 m), South Island (200–860 m). Known from Fiordland, Westland and Western Nelson EPs, the northern limit at Stockton Plateau.

The species typically occurs in scrub or stunted forest where light levels are moderately high, over peaty ground and may form low cushions or mounds, or grow over hummocks formed by mosses and other hepatics. On Stewart Island the species occurs near sea level at the type locality (Port Pegasus, near Belltopper Falls) under *Leptospermum scoparium* and *Dracophyllum longifolium* scrub and is common at that locality. At higher elevations on Stewart Island (330–340 m at Pryse Peak) it forms pure, deep cushions in an open forest that includes stunted *Dacrydium cupressinum*, *Podocarpus hallii*, *Olearia colensoi*, *Gahnia*, *Blechnum* and bryophyte cushions on the forest floor. It reaches its upper altitudinal limit at 600–690 m at the Mt. Rakeahua summit area, occurring in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* from 0.5 m to 2 m tall and significant areas of exposed rock; at this site the species formed a large mound with *Riccardia* sp. and *Eotrichocolea* admixed.

In Fiordland, it is recorded from Doubtful Sound Track at 455–490 m with *Treubia lacunosa*, *Haplomitrium gibbsiae*, *Lembidium nutans*, *Pseudocephalozia lepidozioides*, *Lepidozia* spp. and *Riccardia* spp. (Schuster, 1980a). At Omoeroa Saddle (Westland Natl. Park, 330 m) the species occurs in a bog with shrub heath vegetation that includes *Juncus*, *Carex* and stunted *Libocedrus bidwillii* surrounded by mature *Dacrydium cupressinum* forest. At this site it is found on the bog floor or, at times, on low-lying mounds. It also occurs at 860 m in the Alexander Ra. At Sewell Peak it occurs in extensive hummocks under stunted *Nothofagus solandri* var. *cliffortioides* and *Halocarpus biformis* forest near treeline, with *Bazzania adnexa*, *Breutelia pendula*, *Dicranoloma billardierei*, *D. robustum*, *Heteroscyphus billardierei*, *Hymenophyllum multifidum*, *Hypnodendron colensoi*, *Lepidozia kirkii*, *Luzuriaga parviflora* and *Riccardia cochleata*.

Comments: *Megalembidium* may easily be mistaken for *Isolembidium* and to a lesser extent *Kurzia tenax*, both of which occur in New Zealand. The three genera are similar in plant organization, with a basal, prostrate, branched, stoloniferous, leafless system from which arises an erect, dendroid, 2–3-pinnate, photosynthetic system ± determinate in height, the stem and its branches resembling a "megaphyll." Moreover, in all three the erect photosynthetic system is comprised of terminal branches of both *Frullania* and *Microlepidozia* types (see Fig. 118: 1 [*Megalembidium*] and Fig. 111: 1 [*Isolembidium*]). The three species may be distinguished by the following key:

1a. Stem with a persistent hyaloderm; leaves 5–7-lobed to 0.7, with pluricellular finger-like processes at the juncture of leaf base and stem; leaves of main axis with orientation similar above and below the level of branches; leaves lacking swollen cells distally . . . . . *Kurzia tenax*

1b. Stem with a large-celled hyaloderm that eventually collapses + a subepidermal layer of several thick-walled, pigmented cells and a leptodermous medulla (Fig. 119: 1 [*Megalembidium*]); leaves unlobed or 4-lobulate to ca. 0.15, without finger-like processes at leaf base; leaves of main axis spreading distal to onset of branches but clasping the stem below the level of branches (Fig. 118: 1 [*Megalembidium*] and Fig. 111: 1 [*Isolembidium*]); leaves with swollen cells distally: in *Megalembidium* in lobes of leaves distal to onset of

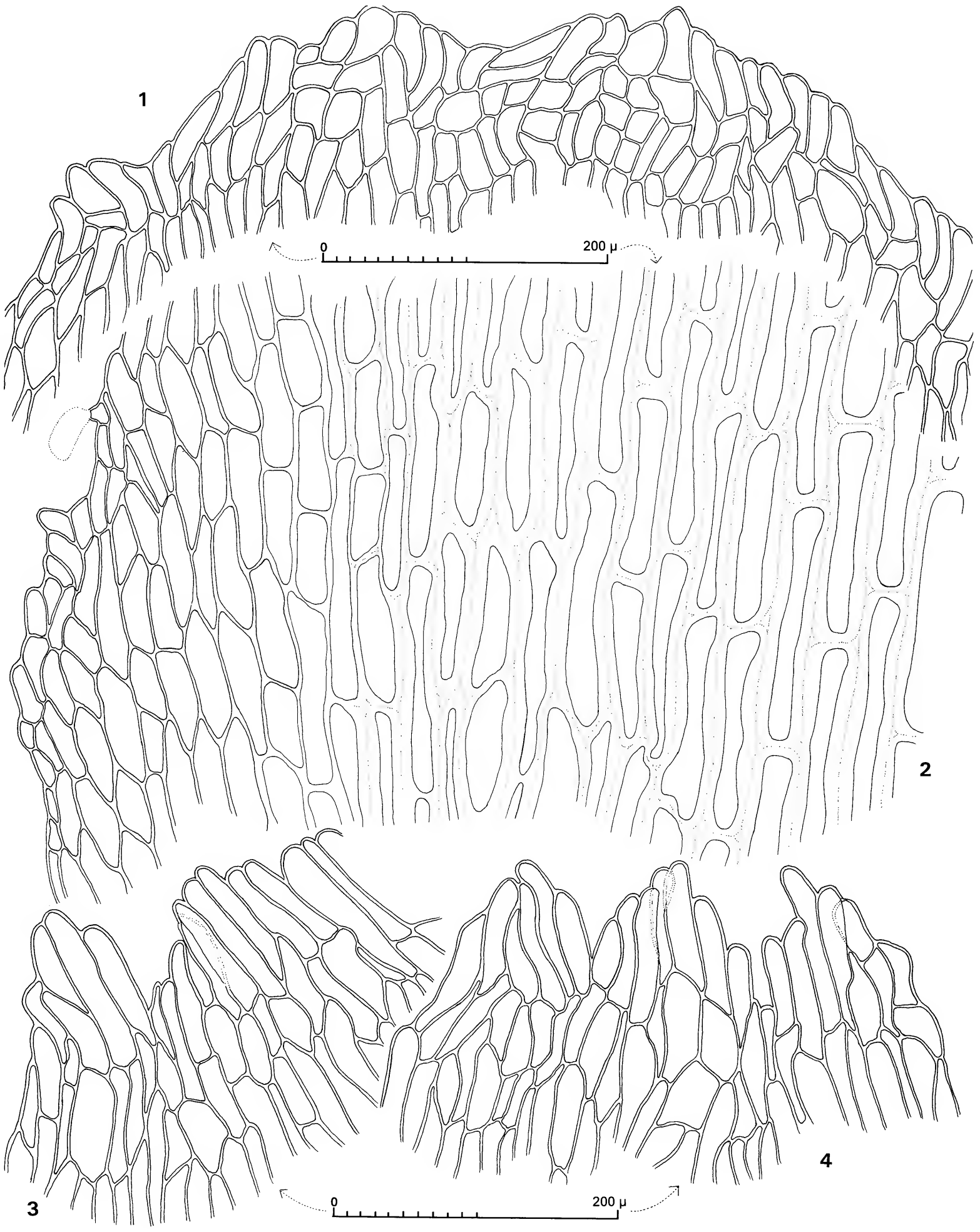

Fig. 120.
Megalembidium insulanum (W.Martin & E.A.Hodgs.) R.M.Schust. 1. Distal portion of ♀ bract. 2. Portion of ♀ bract showing thin-walled marginal cells and exceedingly thick-walled cells in a large median field. 3, 4. Portions of perianth mouth. (All from *Braggins 98474C*, New Zealand, Westland Natl. Park, Omoeroa Saddle.)

branches (Fig. 119: 3), in *Isolembidium* at leaf apex and often also along margins (Fig. 111: 3, 4, 7) 2

2a. Leaves of main erect shoot unistratose, ovate (Fig. 119: 2A, B), those below onset of branches weakly to distinctly imbricate and hiding the stem (Fig. 118: 1); leaf apex 4-lobulate; oil-bodies lacking; antheridial stalk variable, unistratose throughout or at times locally bistratose (Fig. 119: 5–7) . . . . . *Megalembidium*

2b. Leaves of main erect shoot polystratose, broadly ovate-subrotundate to reniform-rotundate in outline (Fig. 111: 1, 2), those below onset of branches remote (Fig. 111: 1); leaf apex undivided; oil-bodies present at least in cells of leaf middle (Fig. 113: 3); antheridial stalk biseriate (Fig. 111: 5) . . . . . *Isolembidium*

Megalembidium is placed in subfamily *Lepidozioideae* by Schuster (1979a, 1980c, 1984e, 2000a). However, Engel and Braggins (2005) demonstrated that the genus should be removed from the *Lepidozioideae* and placed in an independent subfamily. Engel and Braggins (2005) also discussed the similarities of *Megalembidium* to *Isolembidium* of subg. *Lembidioideae*. A remarkable characteristic of the sporophytes of *Megalembidium* is the spiral dehiscence of the capsule wall (Fig. 118: 2, 3). Spiral capsule dehiscence also occurs in most members of the suborder *Balantiopsidinae* (*sensu* Schuster, 1973; see also Engel and Merrill, 1997), some *Calypogeiaceae*, in *Geocalycaceae* (*Saccogynidium*) and in *Plagiochilaceae* (*Plagiochila gigantea*).

Family **CALYPOGEIACEAE** Arnell

Calypogeiaceae Arnell *in* Holmberg, Skand. Fl. 2: 189. 1928.

Plants anisophyllous, closely prostrate and creeping, usually closely attached to substrate, dorsiventrally aplanate, pale to whitish green to yellow-green to (*Mnioloma*) brownish, medium-sized (to 1.8 mm wide in ours). Branching sparing and irregular, the branches predominantly of ventral-intercalary type; *Frullania*-type branches sparing to common in many taxa, or lacking (*Mnioloma*); *Acromastigum*- or *Microlepidozia*-type branches present in a few, exotic taxa; ventral-intercalary stolons absent or if present (*Mnioloma*), then rhizoidous, microphyllous and geotropic. Stem soft-textured, essentially undifferentiated, the cortex ill-defined, at most with 1 layer of ± firm-walled cells. Rhizoids from basal cells of most underleaves. Leaves laterally strongly and widely spreading, the insertion strongly incubous, nearly longitudinal, nearly straight but arched at the dorsal end and extending to stem midline or nearly so (at most with 2 rows of leaf-free cortical cells), the leaves usually ovate to ovate-triangular, infrequently ellipsoidal, broad-based, plane or slightly convex, undivided and usually entire (in some taxa bidentate), the margins entire. Cells (intramarginal) of leaves usually large, subisodiametric or feebly elongated at leaf bases, thin-walled, with trigones lacking, or, less often, small, rarely nodulose; surface smooth or sometimes weakly papillose. Oil-bodies 2–11(13) per cell, colorless to smokey grey to brownish grey, bluish in a few species, finely to coarsely botryoidal. Underleaves distinct, typically 0.2–0.4× area of lateral leaves, inserted on a ± acroscopically arched line, the apex bifid to feebly retuse and then with the lobes each reduced to a slime papilla; lamina margins at times with a strong lateral tooth on one or both sides; underleaves at base with a large, dense, small-celled, rhizoid-initial area, the rhizoid-initials at first forming prominent cushions. Asexual reproduction (*Calypogeia*) by 2-celled, pale green gemmae from malformed and reduced leaves of erect, gemmiparous, tapered shoot apices.

Autoecious (in ours) or, less commonly, dioecious. Androecia on short, ventral-intercalary branches (except *Eocalypogeia* spp.), small, spicate; bracts tiny, pouched; antheridia 1(2–3)

per bract, the stalk 1- or 2-seriate. Gynoecia on very short, leafless, ventral-intercalary branches (except *Eocalypogeia* spp.) that are hidden at the time of archegonial maturation within underleaf axils; gynoecia producing at most 1–2 pairs of reduced bracts or bractlets; sporophyte protected by a conspicuous, pendulous, usually subterranean, densely rhizoidous marsupium (formed after fertilization), the unfertilized archegonia carried down within the marsupial canal; calyptra distinct; perianth lacking.

Seta with 18–20 rows of outer cells, similar in diameter or slightly larger than the many inner cells. Capsule long-ellipsoidal to cylindrical, the valves spirally twisted or not, 2-stratose; outer layer of cells with two-phase development: primary longitudinal and transverse walls lacking thickenings, the primary cells divided 1–3 times by secondary longitudinal walls with nodulose to sheet-like pigmented thickenings; inner layer of cells with numerous semiannular bands.

Spores granular. Elaters nearly straight, hardly tapered at the tips, bispiral.

Type: *Calypogeia* Raddi

A widespread family with four genera. *Eocalypogeia* (R.M.Schust.) R.M.Schust. has two species (Schuster, 1995c); *E. quelpartensis* (S.Hatt. & Inoue) R.M.Schust. is scattered east Asiatic in range (Japan, Korea, Thailand); *E. schusterana* (S.Hatt. & Mizut.) R.M.Schust. is disjunct in Arctic to boreal areas of North America and Asia and is found in Newfoundland, Nova Scotia, west Greenland, Alaska and Siberia (Schuster, 1969c, 1995c, 2000a, p. 489). *Metacalypogeia* (S.Hatt.) Inoue has two species (Schuster, 1995c), *M. cordifolia* (Steph.) Inoue and *M. montana* (Horik.) Inoue, both of Japan (see Inoue, 1959; see also Schuster, 1969c). *Calypogeia* and *Mnioloma* occur in New Zealand.

Calypogeia Raddi

Calypogeia Raddi, Jungermanniogr. Etrusca 31. 1818 (preprint); Mem. Mat. Fis. Soc. Ital. Sci. 18: 42. 1818.
Kantius Gray, Nat. Arr. Brit. Pl. 1: 706. 1821.
Cincinnulus Dumort., Commentat. Bot. 113. 1822.
Parentia Léman, Dict. Sci. Nat. 37: 536. 1825.

Plants usually lax and delicate, typically whitish or pale green, rarely feebly blue-green, lacking brownish pigments, translucent. Branching irregular, remote, mostly ventral-intercalary, leafy and not stoloniform; *Frullania*-type branches usually present, the branches rarely of *Acromastigum* or *Microlepidozia* types. Stem usually with both cortex and medulla thin-walled, rarely with a single-layered cortex of slightly firm-walled cells. Leaves soft-textured, ± hyaline, pellucid, plane or slightly convex, unlobed and entire or bidentate, without a border of differentiated cells. Cells large, rather pellucid, usually very thin-walled and devoid of trigones, or, less often, trigones small, concave-sided, rarely slightly bulging; surface smooth or finely papillose. Oil-bodies 2–10(13) per cell, hyaline, bluish in a few species, botryoidal and usually few-segmented (rarely finely botryoidal). Underleaves typically bilobed, at times unlobed but the lobes each reduced to a slime papilla, the underleaves usually with a conspicuous rhizoid-initial area at base. Asexual reproduction by greenish, delicate, 1–2-celled gemmae from erect, reduced-leaved shoots.

Dioecious or autoecious. Androecia with antheridia 1–2(3) per bract. Marsupium fleshy, cylindrical, pale, densely rhizoidous, the summit with a few, vestigial bractlets.

Capsule cylindrical, the valves spirally twisted, linear, bistratose.

Type: *Calypogeia fissa* (L.) Raddi (≡ *Mnium fissum* L.)

A nearly cosmopolitan genus with ca. 35 species. The genus is recognized here in the more narrowly defined sense of Schuster (1995c, 2000a) that excludes subg. *Caracoma* Bisch. and subg. *Mnioloma* (Herzog) Bisch. About 15 species occur in tropical America (Gradstein et al., 2001) and nine occur in eastern North America (Schuster, 1969c). One species, *Calypogeia sphagnicola*, is bipolar in distribution; in the Southern Hemisphere it is known from southern South America, New Zealand and Tasmania (Schuster, 1969c; Engel, 1978). Bischler (1970) included five species (currently recognized as *Calypogeia*) for South Africa; of these *C. bidentula* (F.Weber) Nees, *C. longifolia* Steph. and *C. microstipula* (Steph.) Steph. are endemic to Africa, *C. arguta* Nees & Mont. is also present in Europe and *C. fissa* (L.) Raddi occurs in Europe and North America. Other species included in the genus by Bischler have subsequently been excluded from the genus.

References: Hodgson (1967); Schuster (1969c, 1995c, 2000a).

Calypogeia sphagnicola (Arnell & J.Perss.) Warnst. & Loeske

[Plate 11D; Fig. 121]

Kantia sphagnicola Arnell & J.Perss., Rev. Bryol. 29: 26. 1902. *Calypogeia sphagnicola* (Arnell & J.Perss.) Warnst. & Loeske, Verh. Bot. Ver. Brandenburg 47: 320. 1905. *Cincinnulus trichomanis* var. *sphagnicolus* (Arnell & J.Perss.) Meyl., Bull. Herb. Boissier, ser. 2, 6: 499. 1906. *Calypogeia trichomanis* var. *sphagnicola* (Arnell & J.Perss.) Meyl., Rev. Bryol. 36: 53. 1909. Type: Sweden, Prov. Dalarna, Mora, *J. Persson*.

Plants closely creeping, pale to whitish green, pellucid, nitid, medium, to 3.1 mm wide. Branching variable, the branches of both ventral-intercalary and *Frullania* types, the intercalary branches somewhat more common, exceptionally *Microlepidozia*-type branches present. Stems soft-textured, without differentiation of a cortex, all cells leptodermous. Leaves remote to loosely imbricate, plane to more often slightly convex, the apices usually gently decurved, mostly asymmetrically ovate-deltoid, broad-based, tapered to a subacute to narrowly rounded to at times retuse, entire apex, about as wide as long to a little longer than wide, 900–1300 μm wide × 1050–1350 μm long. Cells thin-walled, with trigones minute to small and concave-sided, median leaf cells 31–43(48) μm wide × 38–50 μm long; surface smooth. Oil-bodies (*fide* Schuster, 2000a) mostly 5–9 per cell, coarsely botryoidal or few-segmented, a few homogeneous. Underleaves remote to contiguous, 2.2–2.8× stem width, bifid to within 4–7 cells of the rhizoid-initial sector, the lobes acute or subacute. Gemmae ellipsoidal, 2-celled at maturity. Fungal partner an ascomycete.

Plants autoecious. Androecia small, compact spicate; bracts in 3–5 pairs. Marsupia with several bractlets at the summit.

Capsule (*fide* Hodgson, 1967) bistratose; outer layer of cells with incomplete two-phase development: alternating longitudinal walls with continuous sheets of wall material and nodular

to spur-like thickenings; inner layer of cells with numerous semiannular bands, the bands wide, closely spaced, nearly all complete.

Distribution and Ecology: *Calypogeia sphagnicola* is one of a small number of basically Holarctic species that are bipolar in distribution, with isolated stations in the cool to cold southern temperate zones (cf. Schuster, 1969c, 1984b). In the Southern Hemisphere known from New Zealand: South Island (145–1180 m); and southernmost South America (Schuster, 1969c; Engel, 1978). In New Zealand known from Fiordland, Otago, Westland and Western Nelson EPs.

In the Northern Hemisphere with gaps in range, but frequently found in extensive bogs and moors and often abundant, occurring northward into the Arctic, southward throughout areas with extensive conifer forests.

In New Zealand known from a limited number of South Island stations. In Fiordland it occurs at 305 m in Borland Bog near Lake Monowai amongst *Sphagnum cristatum*, with *Kurzia calcarata* and a *Riccardia* species. Also known from the summit of Swampy Hill (N of Dunedin, 600 m) among *S. cristatum* and *S. falcatulum* with *K. calcarata*, *Pulchrinodus inflatus* and *Riccardia*, as well as on dripping roadside banks with *Balantiopsis tumida*, *Breutelia pendula*, *Campylopus clavatus*, *Lembidium nutans* and *Warnstorfia fluitans*. At the summit plateau of Mt. Maungatua (30 km W of Dunedin, 825 m), over wet peaty soil near the edge of a bog in tussockland with a mosaic of scattered bogs having abundant *Sphagnum* and patches of *Dracophyllum*, *Halocarpus bidwillii*, *Hebe* and *Donatia novae-zelandiae*. Not always associated with *Sphagnum*: occurring, for example, on bank of a streamlet through a thicket of *Leptospermum scoparium* and *Ulex europaeus* in the Paparoa Ra. (N side of Tiropahi River, 145 m). On Garibaldi Ridge (Western Nelson EP, 1180 m) it was found in a *Schoenus pauciflorus – Bulbinella hookeri* sedgeland just above treeline, on soil and sedge leaf litter, with *Anisotome aromatica*, *Breutelia pendula*, *Clasmatocolea* sp., *Dicranoloma robustum*, *Fissidens adianthoides* and *Cheilolejeunea mimosa*.

Comments: A variable plant in the Holarctic, where three forms are recognized by Schuster (1969c); only a small part of the range of variation exists in the south temperate. The distichous-leaved, pale to whitish green shoots, with asymmetrically ovate-deltoid, somewhat ovate or ovate-triangular, bluntly pointed, incubous leaves can hardly be confused with any other regional species. Several species of *Radula* are similar in aspect in dorsal view due to the incubous, longitudinally inserted, unlobed and entire leaves and comparable plant size. That genus is devoid of underleaves and the leaf has a small ventral lobule. *Bazzania* may have similar unlobed leaves, but is nearly always tridentate-leaved, is much firmer-textured, at times brownish pigmented and bears conspicuous ventral-intercalary stoloniform branches. This species, like almost all basically Holarctic species that have a bipolar distribution, is dioecious.

Rodway (1916) described *Calypogeia tasmanica* Rodway (Pap. & Proc. Roy. Soc. Tasmania 1915: 107. 1916; type: Tasmania, Adamson's Peak). Schuster (1969c, p. 135) stated that he "[could] find no real differences between the plant from Tasmania . . . and *C. sphagnicola*." The status of *C. tasmanica* should be evaluated prior to a formal placement of the species in the synonymy of *C. sphagnicola*.

The species description above was fashioned to include only New Zealand populations of the species.

Hodgson (1967) included figures of the capsule wall that were accredited to George Scott. These figures are the only source of sporophyte data, as Hodgson did not provide a descrip-

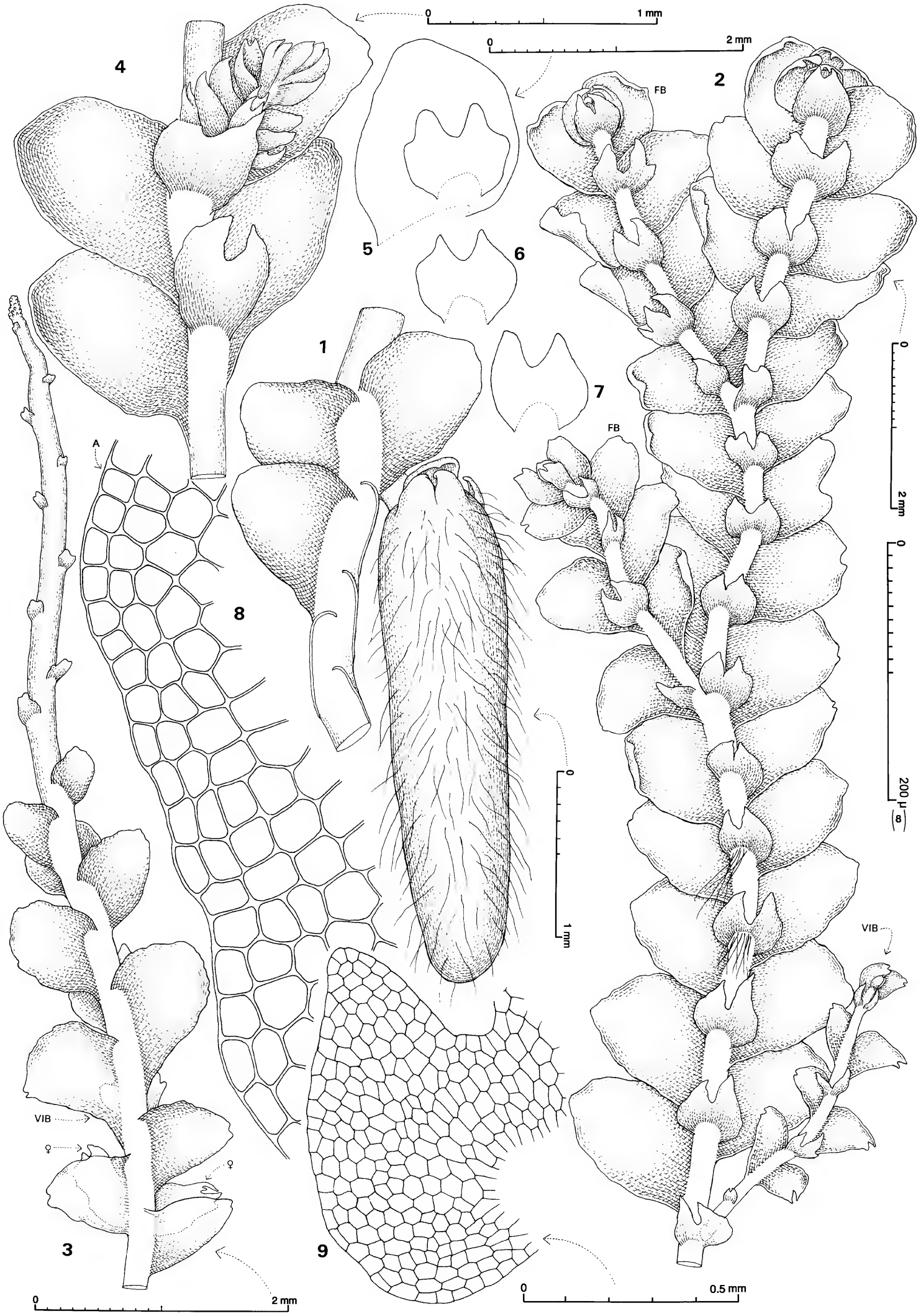

Fig. 121.
Calypogeia sphagnicola (Arnell & J.Perss.) Warnst. & Loeske. 1. Portion of main shoot with marsupium, dorsal view. 2. Portion of main shoot (ventral view) with 2 *Frullania*-type branches (= FB; note first branch underleaf) and a ventral-intercalary branch (= VIB); rhizoids shown in part. 3.

tion of the capsule, spores or elaters. Unfortunately the collection from which the figures were drawn is not cited and a New Zealand provenance is uncertain.

Mnioloma Herzog

Mnioloma Herzog, Ann. Bryol. 3: 119. 1930. *Calypogeia* subg. *Mnioloma* (Herzog) Bisch., Candollea 18: 25. 1963 (1962).

Plants dull, opaque, light brown to yellowish brown to golden, the stems deeper brown, the shoots markedly flat. Branching irregular, the branches all ventral-intercalary, leafy or stoloniform and long, geotropic, microphyllous and copiously rhizoidous. Stem with cortex in 1(2) rows of firm- to thick-walled cells slightly smaller than those of the medulla; medullary cells thin-walled, hyaline. Rhizoids normally lacking on leading leafy shoots, typically only present at bases of underleaves and leaves of stoloniform branches. Leaves dull (but the border at times nitid), notably plane, ovate-deltoid to (mostly) oblong-ovate to oblong, the apex typically rounded, contracted to a beaked or pointed tip (*Mnioloma rhynchophyllum*), unlobed or (*M. retusa*) retuse to shallowly bilobed; leaves with a border of differentiated cells (rarely feebly developed or lacking), the border cells slightly to conspicuously elongated either at right or oblique angles to the margin, in some species the margin crenulate to denticulate by projecting free ends of the marginal cells, the cells of the border often thicker-walled, lacking oil-bodies and chloroplasts, and with a smooth surface. Cells (intramarginal) thin- to feebly firm-walled, trigones small to exceptionally bulging and nodulose; surface papillose. Oil-bodies usually lacking in marginal cells, (1)2–11(13) per cell, colorless to smokey grey to brownish grey, finely botryoidal. Underleaves delicate, hyaline and echlorophyllous, orbicular-ovate to elongate-ovate, ± convex (ventral view); apex mostly feebly emarginate or a mere weak notch, the vestigial, closely juxtaposed lobes each reduced to a slime papilla, the sinus very small, the underleaves bilobed to 0.6 in a few species; cells thin-walled, usually markedly elongated, often ± prosenchymatous at the margins, the marginal cells often widest at the radial walls and with the intervening free wall arched toward the cell lumen, the margins thus appearing scalloped. Asexual reproduction lacking.

Dioecious. Androecia on very short, ventral-intercalary branches ± hidden in axil of underleaves, compact; bracts in 1–2 pairs, bilobed. Marsupium fleshy, cylindrical, brownish, rhizoidous, the summit with a few, vestigial bractlets.

Capsule cylindrical, the valves spirally twisted, linear, outer layer of cells markedly elongated, with two-phase development: primary longitudinal and transverse walls lacking thickenings, the secondary longitudinal walls with thickenings feebly sinuous-nodular; inner layer of cells with semiannular bands narrow, complete or, mostly, incomplete.

Spores granular. Elaters tortuous, bispiral.

Portion of gemmiparous shoot, with, toward base, 2 young marsupia (= ♀, shown in outline); dorsal view. 4. Portion of main shoot with androecium, ventral view. 5–7. Leaf and underleaves, all drawn to same scale. 8. Portion of leaf apex (= A) and distal portion of ventral margin (drawn to scale at right of figure). 9. Lateral half of underleaf. (Fig. 1, from *Allison 13031*, New Zealand, South Is., Otago EP, Swampy Hill [MPN]; 2, 3, 5–9, from *Engel 17719*, New Zealand, South Is., Otago EP, summit plateau of Mt. Maungatua; 4, from *Child H2528*, New Zealand, South Is., Otago EP, Swampy Hill summit.)

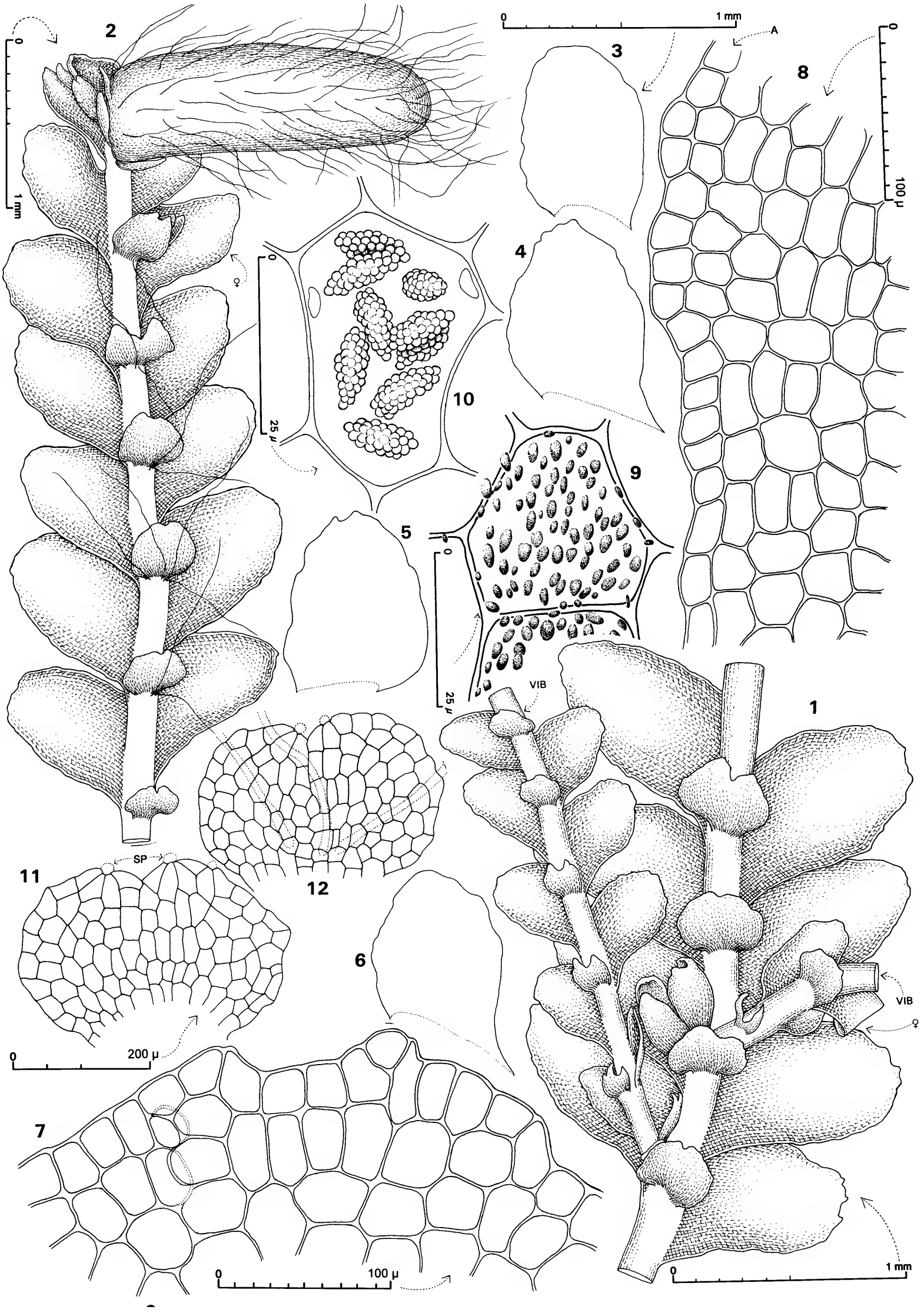

Fig. 122.
Mnioloma novaezelandiae J.J.Engel. 1. Portion of main shoot with 2 ventral-intercalary branches (= VIB) and a young gynoecium (= ♀), ventral view. 2. Portion of main shoot with marsupium and

Type: *Mnioloma rhynchophyllum* Herzog

A pantropical genus of ca. 13 species, 11 of which are restricted to the Neotropics and mostly occur in northern South America, Central America and the West Indies. The genus is absent from southern South America. *Mnioloma fuscum* (Lehm.) R.M.Schust. has a broad pantropical distribution that includes South Africa and New Guinea. *Mnioloma novaezelandiae* is endemic to our area.

References: Engel (2006c), Renner (2003), Schuster (1995c, 2000a).

Mnioloma novaezelandiae J.J.Engel

[Figs. 122, 123: 1–3]

Mnioloma novaezelandiae J.J.Engel, Cryptogamie 27: 111. *f. 1; 2: 1–3.* 2006. Holotype: New Zealand, South Is., Southland Land District, Fiordland Natl. Park, Charles Sound, south side of Gold Arm, 340 m, 8 April 2002, *Renner CMS J156 T/10* (F); isotype: (CHR).

Plants rather flexuous, procumbent, distinctly brownish, the stems more deeply so, the shoots medium in size, to 1.6 mm wide. Branching frequent, irregular, uniformly ventral-intercalary, at times 2 per underleaf axil, the branches uniformly leafy in some populations, one population with branches leafy as well as stoloniform, geotropic and whip-like. Stems conspicuously striolate in surface view, in cross section with cortex in 10–16 rows, in an ill-defined layer of slightly thickened, markedly brown-pigmented cells; medullary cells with walls thin, pigmented or not. Rhizoids hyaline or pale brown, at immediate base of underleaves, few per underleaf base or sporadic, the rhizoid surface finely but distinctly roughened, the apices at times dendritic. Leaves virtually flat, widely spreading, contiguous to weakly imbricate, the insertion not extending to stem midline dorsally, delimiting a leaf-free strip of 2 cells wide, the stem widely exposed in dorsal view; leaves ovate-oblong to rounded-quadrate, on mature shoots 480–600 μm wide × 600–730 μm long; apices broadly rounded to truncate, often unevenly repand, sporadically retuse; margins often unevenly repand, especially the dorsal, otherwise entire, the free tangential wall of marginal cells straight or somewhat bulging, the margin not crenulate and not with marginal cells widest at the radial walls and with the intervening free wall arched toward the cell lumen; leaves with apex and margins with 1(2) rows of marginal cells mostly subisodiametric, smaller than intramarginal cells and forming an incipient border, the marginal cells with free wall straight to bulging to, at times, angularly projecting (particularly toward the distal end of the free wall), making the margin locally minutely denticulate, the marginal cells sporadically somewhat radially elongated (to 2.2:1), especially toward the leaf bases, but these cells on the whole narrower than intramarginal cells and contributing to the aspect of a border of differentiated cells. Cells of median sector of leaf thin-walled, trigones absent or minute, the cells 25–36 μm wide × 34–49 μm long; surface conspicuously papillose, the surface becoming striate toward basal cells. Oil-bodies occupy-

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a young female inflorescence (= ♀), ventral view. 3–6. Leaves (all drawn to same scale). 7. Portion of leaf apex showing marginal row of smaller cells. 8. Portion of apex (= A) and dorsal lateral margin of leaf showing marginal row of smaller cells. 9. Median leaf cells showing surface papillae. 10. Median leaf cells with oil-bodies and a few chloroplasts. 11, 12. Underleaves; rhizoids shown with stipple at right; note small slime papillae (= SP). (Figs. 1–9, 11, 12, from type; 10, from *Glenny 8876*, New Zealand, Westland EP, Mt. Te Kinga.)

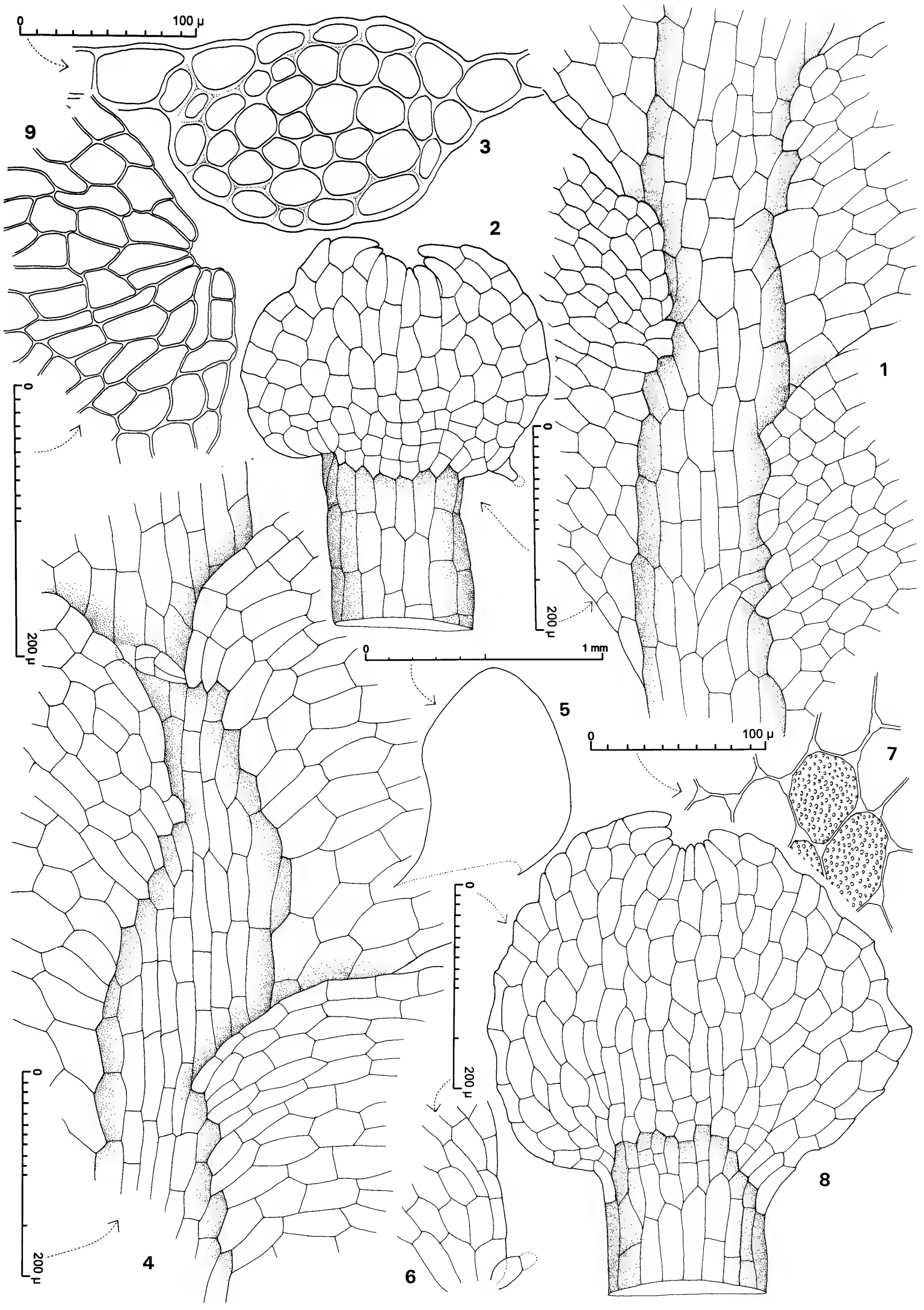

Fig. 123.
Mnioloma novaezelandiae J.J.Engel (1–3) and *M. fuscum* (Lehm.) R.M.Schust. (4–9). 1. Portion of leading shoot showing leaf bases (dorsal view); note that the insertion lines delimit a leaf-free strip of 2 stem cells wide. 2. Portion of stem with underleaf; note ventral merophyte width of 6

ing conspicuous portion of volume of lumen, smokey grey, 6–11(13) per cell in median portion of leaf, narrowly elliptic to fusiform, less often broadly elliptic, some globose, finely botryoidal, 4.8–6.2 × 10.6–16.3 μm, broadly elliptic ones 5.8 × 8.2 μm, the globose ones 5.8–6.2 μm in diam. Underleaves inserted on 4–5 rows of stem cells, 1.7–2.6× stem width, distant, slightly convex (ventral view), oblate to reniform, the apices equally or unequally bilobed to retuse, the lobe apex often rounded, each with a slime papilla, the 2 papillae often closely juxtaposed, the cells ringing the sinus not much differentiated from those below or if elongated, then not much narrower; the sinus often notch-like; margins entire, the free tangential wall of marginal cells straight or somewhat bulging, locally and sporadically imperceptibly crenulate via marginal cells widest at the radial walls and with the intervening free wall arched toward the cell lumen. Asexual reproduction lacking.

Dioecious. Androecia unknown. Gynoecia on very short ventral-intercalary branches, bud-like when unfertilized. Marsupium fleshy, cylindrical, brownish, similar in pigmentation to stem, rhizoidous, the summit with a few, vestigial bractlets.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (120–340 m), North Island (ca. 800–840 m). Known from Fiordland, Westland and Auckland EPs.

Known only from a few sites, one in the southwestern sector of South Island (type), in Westland (Mt. Te Kinga) and Coromandel Peninsula (Mt. Moehau). On Mt. Moehau plants occurred on soil admixed with *Psiloclada clandestina* and *Bazzania tayloriana* deep in a protected pocket of a vertical bank at ca. 800–840 m in an area of rocky outcrops and shrub-heath communities including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus* and *Corokia buddleioides*. The type occurred at 340 m on a soil bank in a forest dominated by *Nothofagus menziesii*, *N. solandri* var. *cliffortioides* growing with *Zoopsis argentea*, *Bazzania adnexa* and *Tylimanthus tenellus* (see Renner, 2003). The Mt. Te Kinga specimen occurred on a wet soil bank under *Blechnum colensoi* and *B. novaezelandiae*, in *Dacrydium cupressinum* and *Weinmannia racemosa* forest. It was growing with *Leptopteris superba*, *Microlaena avenacea*, *Metrosideros diffusa*, *Nertera dichondrifolia* and the bryophytes *Cryptopodium bartramioides*, *Distichophyllum kraussei*, *Lepidozia spinosissima*, *Leucobryum candidum*, *Psiloclada clandestina* and *Zoopsis setulosa*.

Comments: *Mnioloma* was first reported for New Zealand by Renner (2003), who used the name *Mnioloma fuscum*, a broadly distributed species. Engel (2006c) recognized the New Zealand population as a distinct species and differentiated it from *M. fuscum* on the basis of leaf and underleaf characters, the presence of a dorsal leaf-free "gutter," as well as differences in ventral merophyte number. In the field the species has the appearance and habitat of the moss genus *Distichophyllum*. On closer examination, it resembles a *Bazzania* in color, size and the shape of the underleaves, but the leaf apices are repand or entire rather than 3-fid.

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cells. 3. Stem, cross section. 4. Portion of leading shoot showing leaf bases (dorsal view); note that the insertion lines extend to the stem midline; note also the tooth at base of leaf at upper right. 5. Leaf. 6. Dorsal base of leaf with 1-celled tooth capped by a slime papilla. 7. Median leaf cells, the papillose surface shown in part. 8. Portion of stem with underleaf; note ventral merophyte width of 13 cells. 9. Underleaf apex showing the minute notch and the differentiated cells ringing the sinus. (Figs. 1–3, from type of *M. novaezelandiae*; 4–9, from type of *M. fuscum*.)

Suborder 5. **TRICHOTEMNOMATINEAE** J.J.Engel

Jungermanniales suborder *Trichotemnomatineae* J.J.Engel, Nova Hedwigia 80: 374. 2005.

Family **TRICHOTEMNOMACEAE** R.M.Schust.

Blepharostomataceae subfam. *Trichotemnomoideae* R.M.Schust., Candollea 21: 65. 1967 (1966), *nom. inval. Trichotemnomaceae* R.M.Schust., J. Hattori Bot. Lab. 36: 340. 1973 (1972).

Plants strongly anisophyllous, soft and spongy, prostrate, creeping and forming loose, wool-like tufts or mats, light to yellow-green, rather small, to 2.3 mm wide. Branching sparing, irregular, usually ventral-intercalary, occasionally of *Frullania* type. Stems with cortex in 1(2) layers of smaller cells with slightly thickened, often light brownish walls; medullary cells with walls thin. Rhizoids sparse, commonly altogether lacking, colorless, in tight fascicles from stem at immediate base of underleaves, the tips digitate, nonseptate. Leaves loosely imbricate, strongly succubously inserted, the lines of insertion extending to stem midline dorsally, slightly recurved at ventral end, the leaves undulate-crispate, 1100–2250 μm wide × 1300–1650 μm long, asymmetrically basically 4-lobed to 0.35–0.5, but often with several accessory lobes, the lobes all incurved, the ventral lobes larger than the dorsal and gently and broadly incurved, the dorsal-most 1 or more lobes somewhat smaller and often more sharply incurved. Lobes canaliculate (at least toward base), long-attenuate to narrowly acute, gradually tapered to a terminal, caudate, often arcuate or tortuous cilium consisting of a uniseriate row of 5–8 cells, the cells of the cilium firm-walled and with projecting septa, strongly and narrowly elongated (to 8:1), the terminal cell of uniseriate row finely tapering to a sharp point and thickened at the tip; margins of lobes recurved, armed with pairs of opposing cilia oriented at ± right angles to the lobe and often ultimately curved, the cilia 2–5 cells broad at the base, the distal portion of cilia similar to that of the lobe tips, the lower armature laciniiform; sinuses between lobes sharply recurved. Disc asymmetric, highest in ventral half, the margins on each side with a few lacinia and cilia, the ventral margin reflexed. Cells of disc irregularly arranged or in partial, ill-defined tiers, oblong-hexagonal to rectangular, the walls thin, with trigones large and slightly to moderately bulging, the surface of non-ciliate portion of lobes distinctly striate-papillose, of disc distinctly long-striate, of cilia obscurely papillose (especially the distal cells). Oil-bodies in all leaf cells dimorphic: one type, 2–4 per median leaf cell, burnt orange-brown, large, coarsely granular-finely papillose, irregular in shape, often broad-elliptic, some potato-shaped, others subcrescentic, often appearing to have a rather long, longitudinal fold or pinch, 5.3–7.2(8.6) × 12–13.4 μm, a few globose and 5.8 μm in diam.; the other type in outer part of cytoplasm, hyaline, numerous per cell, ± spherical, homogeneous, smooth and much smaller (only 1–1.9 μm in diam.). Chloroplasts smaller than smooth oil-bodies. Underleaves ca. 0.5× leaf size or a little more, deeply bifid, the lobes canaliculate and with cilia and lacinia as in leaves; disc concave (ventral view), the margins on each side with a few cilia and a small, accessory lobe. Asexual reproduction lacking.

Dioecious. Androecia spicate, at times ± vermiform, small and inconspicuous, on highly abbreviated, determinate, ventral-intercalary branches that lack normal vegetative leaves; bracts in 3–7 pairs, ventricose-inflated, ± equally 4-fid, or bifid and with a lacinia on each side, the disc with cells with small trigones, the lobes abruptly becoming ciliiform distally, the cilia shorter than those of leaves and comprised of firm-walled cells with projecting septa; antheridia (1)2–3 per bract, the stalk short, 5–6 cells long, biseriate, the body with 2 irregular

tiers of cells; bracteoles lacking antheridia, slightly convex (ventral view), 2(3)-lobed, the lobes entire or with a few small teeth, the disc entire. Gynoecia on short, abbreviated, ventral-intercalary branches lacking normal leaves, with 3 rings of scale-like perigynial bractlets, the bractlets each laciniate-lobulate and with each lobe or lacinia terminating in a cilium similar in form to those of the leaf lobe tips; no tubular perianth forming, but instead, a pendent, cylindrical, fleshy, pale green marsupium develops that is densely covered by colorless rhizoids. Calyptra distinct, carried down within the marsupium, the sterile archegonia remaining at extreme base and not lifted part way up the calyptra (i.e., a shoot-calyptra lacking).

Foot with elaboration of an irregular, sheet-like, haustorial collar with a scalloped free margin. Seta with 26 rows of outer cells surrounding an inner core of ca. 42 scattered cells of ± similar size. Capsule seen only in immature stage, long-ellipsoidal, the wall 30–34 μm thick, of 2 (locally 3) layers; outer layer of cells subquadrate to short-rectangular, to 1.7× size of innermost layer.

A family with one genus, *Trichotemnoma*, of New Zealand and Tasmania.

Trichotemnoma R.M.Schust.

Trichotemnoma R.M.Schust., Nova Hedwigia 15: 440. 1968. *Trichotemnoma* R.M.Schust., J. Hattori Bot. Lab. 27: 150. 1964, *nom. inval.*, *sin. descr. lat.*

Type: *Trichotemnoma corrugatum* (Steph.) R.M.Schust. (≡ *Blepharostoma corrugatum* Steph.)

Monotypic.

References: Engel (2005b); Hodgson and Allison (1962); Schuster (1964c, 2000a).

Trichotemnoma corrugatum (Steph.) R.M.Schust.

[Plate 4E, F; Fig. 124]

Blepharostoma corrugatum Steph., Hedwigia 32: 315. 1893 ("*corrugata*"). *Temnoma corrugatum* (Steph.) R.M.Schust., Bryologist 62: 240. 1959. *Trichotemnoma corrugatum* (Steph.) R.M. Schust., J. Hattori Bot. Lab. 27: 154. 1964, *nom. inval. Trichotemnoma corrugatum* (Steph.) R.M.Schust., Nova Hedwigia 15: 440. 1968. Type: New Zealand, Stewart Is., *Kirk 266* (MPN, hb. Hodgson no. 13920, *non vidi*).

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island, South Island (0–1300 m); Australia: Tasmania. In New Zealand known from Fiordland (Preservation Inlet, Dusky Sound, Milford, West Arm of Lake Manapouri), Westland (Omoeroa Saddle, Hohonu Ra. and Tiropahi River) and Western Nelson (Paparoa Ra., Te Kuha ridge, Denniston and Stockton Plateau) EPs, the northern limit at Stockton Plateau.

In New Zealand the species has a local and sporadic distribution in niches where desiccation never occurs. It rarely is found on the floor of forests of *Nothofagus*, *Metrosideros umbellata*, *Archeria traversii* and *Lepidothamnus intermedius*. More commonly it occurs under *Leptospermum scoparium* scrub that grades into *Leptospermum* shrublands and open pakihi dominated by *Empodisma minus* and *Gleichenia microphylla*. It is rarely found in the penalpine

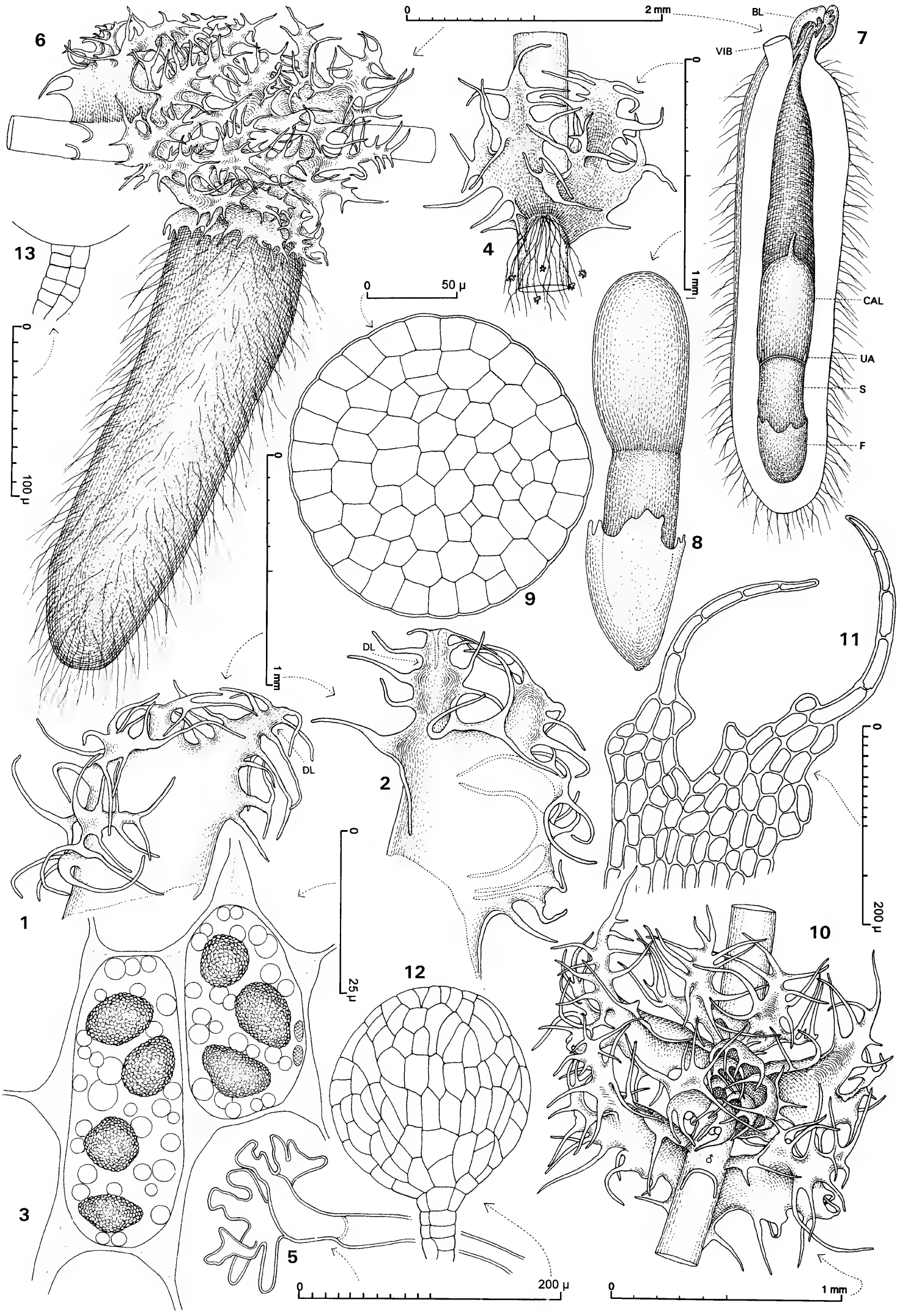

Fig. 124.
Trichotemnoma corrugatum (Steph.) R.M.Schust. 1. Leaf, adaxial aspect (DL = dorsal lobe). 2. Leaf, abaxial aspect (DL = dorsal lobe). 3. Cells of disc showing dimorphic oil-bodies, some large and papillose, others small, homogeneous and smooth; note also the chloroplasts (crosshatch

zone under *Chionochloa pallens* tussockland on shaded south-facing hillslopes and it is found at various altitudes on rock faces kept constantly wet by dripping water. For an example of this last habitat, along the track to Bowen Falls at Milford Sound plants occur at sea level and loosely creep and form pure or nearly pure (and then admixed with *Heteroscyphus decipiens*) spongy masses on dripping, exposed, vertical cliffs with a dense bryophyte cover. The species also grows rather exposed at Omoeroa Saddle (Westland Natl. Park). Here it occurred in a bog with shrub heath vegetation that includes *Juncus* sp., *Carex* sp. and stunted *Libocedrus bidwillii* surrounded by mature *Dacrydium cupressinum* forest. At this site plants form small mounds at the sloping sides of small raised areas at the bases of *Libocedrus* saplings; plants occur at the upper reaches of this niche where periodic drying is probable. These raised areas are between wet depressions where standing water is common. At the Omoeroa site the species apparently is restricted to the crest of the boggy area, where some drainage is probable.

Trichotemnoma also occurs under *Gleichenia* in a low-lying, waterlogged, acidic site with poor drainage (pakihi) at White Horse Creek (S of Charleston, ca. 300 m, *leg. John Child*). However, the species also may be found in humid, protected sites. At Monkey Puzzle Gorge (South Westland, 120 m), for example, it occurred very loosely over *Lepidozia spinosissima* and *L. microphylla* in a cave-like area under a tree mass within a forest dominated by *Nothofagus menziesii* and *Dacrydium cupressinum* with some *N. solandri* var. *cliffortioides*; at this site the floor and banks within the forest are dominated by bryophytes. Accompanying species under forest are *Acrobolbus lophocoleoides*, *Archeophylla schusteri*, *Bazzania novae-zelandiae*, *Dicranoloma robustum*, *Hymenophyllum multifidum*, *Lepidozia spinosissima*, *Megalembidium insulanum*, *Schistochila glaucescens*, *Treubia lacunosa* and *Wijkia extenuata*. Accompanying species in a more open pakihi habitat are *Acromastigum anisostomum*, *A. brachyphyllum*, *Dicranoloma robustum*, *Heteroscyphus decipiens*, *Kurzia calcarata*, *Lepicolea scolopendra*, *Lepidozia hirta*, *L. ulothrix*, *Isolembidium anomalum*, *Pleurophascum grandiglobum* and *Saccogynidium decurvum*. In penalpine tussocklands accompanying species are *Adelanthus occlusus*, *Blepharidophyllum vertebrale*, *Breutelia elongata*, *Clandarium xiphophyllum*, *Eotrichocolea polyacantha*, *Gackstroemia alpina*, *Goebeliella cornigera*, *Heteroscyphus mononuculus*, *Radula sainsburiana* and *Riccardia colensoi*.

The habit of *Trichotemnoma* is distinctive: plants are at times rather long, scraggly and not particularly gregarious, while at other times they form soft, spongy, pale to yellow-green pure patches or tufts that can be up to 150 mm in diam.

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shading). 4. Underleaf (*in situ*) showing rhizoids with digitate tips. 5. Rhizoid with digitate tip. 6. Portion of main shoot with marsupium on a short, ventral-intercalary branch, ventral-lateral view; note rings of bractlets at summit of marsupium and also the leaf insertion. 7. Median-longitudinal section of marsupium; note the strongly abbreviated ventral-intercalary branch (VIB), the tuft of bractlets (= BL) at the summit, the calyptra (= CAL), with 2 unfertilized archegonia at the extreme base (one at UA, the other to left), the seta (= S), and the foot (= F), with the scalloped haustorial collar. 8. Young sporophyte, note elaborated, sheet-like haustorial collar. 9. Seta, cross section. 10. Portion of main shoot with androecium in axil of lowermost underleaf, ventral view; note 2 antheridia are visible in axils of each of uppermost bracts (= ♂). 11. Portion of ♂ bract. 12. Antheridium. 13. Antheridial stalk. (Figs. 1, 2, 6–13, from *Engel 22005*, New Zealand, South Is., Fiordland Natl. Park, Milford Sound, track to Bowen Falls; 3, from *Glenny 8910*, New Zealand, South Is., Western Nelson EP, Waimangaroa R.; 4, 5, from *Engel 23197*, same loc. as *Engel 22005*.)

Comments: *Trichotemnoma corrugatum* is a distinct plant and should not be confused with any of our other species. Plants are pale green or a bright yellowish green and do not develop secondary pigments even when growing under exposed conditions; the color is distinctive in the field. In this respect alone it differs from *Temnoma pulchellum*, which it superficially resembles, and other members of that genus, all of which freely develop brownish pigmentation. Plants of *T. corrugatum* may be distinguished by the strongly succubously oriented, undulate-crispate leaves with, basically, 4 lobes, but, typically, several accessory lobes are developed, particularly in well-developed phases. All lobes are incurved, the ventral lobes broadly and gently so, while the dorsal-most lobes are notably sharply incurved (Fig. 124: 1, 2). The leaves are strongly asymmetric, with the ventral half of the disc much higher than the dorsal (Fig. 124: 1, 2). For further discussion, including comments regarding taxonomic placement of the genus, see Engel (2005b).

Suborder 6. **ANTHELIINEAE** R.M.Schust.

Jungermanniales suborder *Antheliineae* R.M.Schust., New Manual Bryol. 2: 981. 1984.

Family **ANTHELIACEAE** R.M.Schust.

Antheliaceae R.M.Schust., J. Hattori Bot. Lab. 26: 236. 1963.

Plants isophyllous, julaceous, closely prostrate, slender and terete, greenish to bluish green to brownish, with age plants often secreting a water-repellent whitish substance and appearing bleached; shoots small to medium in size. Branching usually laxly pinnate, the branches normally of *Frullania* type; *Acromastigum*-type branches rare; ventral-intercalary branches rare, stoloniform. Stems comprised of a moderately well-defined hyaloderm of thin-walled cells that collapse with age and 1–2 subepidermal layers of thick-walled cells that grade into a leptodermous medulla, the stem cells similar in size but the subepidermal cells somewhat smaller. Rhizoids colorless, mostly from underleaf bases, some sporadically scattered over ventral surface of stem. Leaves suberect to erect, transversely inserted, unistratose or locally bistratose, concave, oblong, bifid to 0.5–0.7, the lobes narrowly acute, the lobe and lamina margins entire. Cells, aside from marginal sectors, rectangular, thin- to equally thick-walled, trigones lacking; surface smooth. Oil-bodies lacking. Underleaves identical to leaves in form, size and orientation. Asexual reproduction absent.

Dioecious or (in ours) paroecious. Androecia on leading shoots, becoming intercalary; bracts leaf-like but somewhat ventricose at the base and less deeply lobed; antheridia usually 1 per bract, the stalk biseriate; bracteoles lacking antheridia. Gynoecia terminal on leading shoots, with several progressively larger, closely imbricate bracts and bracteoles that are leaf- and underleaf-like, appressed to the perianth and form a compact bud-like, swollen, abruptly clavate capitulum; coelocaule-precursor distinct, low to rather high, the foot growing down into the shoot tip; shoot-calyptra present. Perianth distinct, ovate to oblong in outline, arising from a stout, swollen stem apex, pluriplicate, contracted at the mouth, often deeply 3–6-lobed.

Seta short, of the general type, with ca. 16–24 rows of outer cells surrounding numerous inner cell rows identical in diameter. Capsule spherical or nearly so, usually only shortly exserted, the wall 2-stratose; outer layer of cells usually subquadrate, never consistently elongated, not tiered, with one-phase ontogeny, all walls (except isolated short ones) with 1–2

strong nodular thickenings; inner layer of cells elongated, with semiannular bands mostly incomplete, occasionally complete, the radial walls also with nodular thickenings.

Spores delicately papillose, 1.5–2.5× elater diam. Elaters short, often tortuous, the ends weakly to strongly tapered, 2 broad or 3 narrow spirals.

Type: *Anthelia* (Dumort.) Dumort.

Anthelia (Dumort.) Dumort.

Jungermannia sect. *Anthelia* Dumort., Syll. Jungerm. Europ. 63. 1831. *Anthelia* (Dumort.) Dumort., Recueil Observ. Jungerm. 18. 1835.

Type: *Anthelia julacea* (L.) Dumort. (≡ *Jungermannia julacea* L.)

The foregoing family description also serves to characterize the only genus.

A family treated here with one genus, *Anthelia*. The genus has two Arctic-alpine species, one, *A. juratzkana* (Limpr.) Trevis., is bipolar in distribution and occurs in our area (see Schuster, 1974a). Some controversy surrounds circumscription of the family. Hässel (1980a) included the monotypic genus *Grollea* R.M.Schust. in the *Antheliaceae*, but (Schuster, 1984e, 2000a) placed it in its own family, *Grolleaceae*. Schuster (1984c, 2000a) placed the *Grolleaceae* in suborder *Herbertineae*. The *Antheliaceae* was placed in the *Cephaloziineae* by Schuster (1973, p. 392).

The genus includes only two species, *Anthelia julacea* (L.) Dumort. and the following. Both occur in the Northern Hemisphere, but *A. julacea* is chiefly oceanic and subarctic or alpine and absent from continental regions, whereas *A. juratzkana* is probably present in all Arctic regions and occurs northward to the farthest edges of land, to at least 82° 30′ N (Schuster et al., 1959, 1974a). The range of *A. juratzkana* extends southward to New Guinea and to New Zealand. In the Americas, it extends, following the Cordillera, to Mexico, Venezuela, Colombia, Ecuador and Bolivia, southward to Tierra del Fuego, South Georgia and the Antarctic Peninsula. Both species occur only in strongly illuminated sites, either north or south of forested regions, or above treeline in alpine situations. Both occur on inorganic substrates, chiefly mineral soils.

References: Schuster (1974a, 2000a).

Anthelia juratzkana (Limpr.) Trevis.

[Plate 11F; Fig. 125]

Jungermannia nivalis Sw. *in* F.Weber & D.Mohr, Index Mus. Pl. Crypt. 5. 1803, *nom. dub.*
Jungermannia juratzkana Limpr. *in* Cohn, Krypt.-Fl. Schlesien 1: 289. 1876. *Anthelia juratzkana* (Limpr.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 416. 1877. Type: Germany, Riesengebirge, *Limpricht*.

Plants stiff and brittle, terete, filiform and slender, densely leafy, often light green toward shoot apices, brownish below, forming thin, loosely gregarious, silvery, bleached whitish small patches or crusts, or as isolated, dwarf, whitish plants, at times suberect and caespitose with other hepatics, minute, to 350 μm wide with leaves. Branching remote and with 1–4

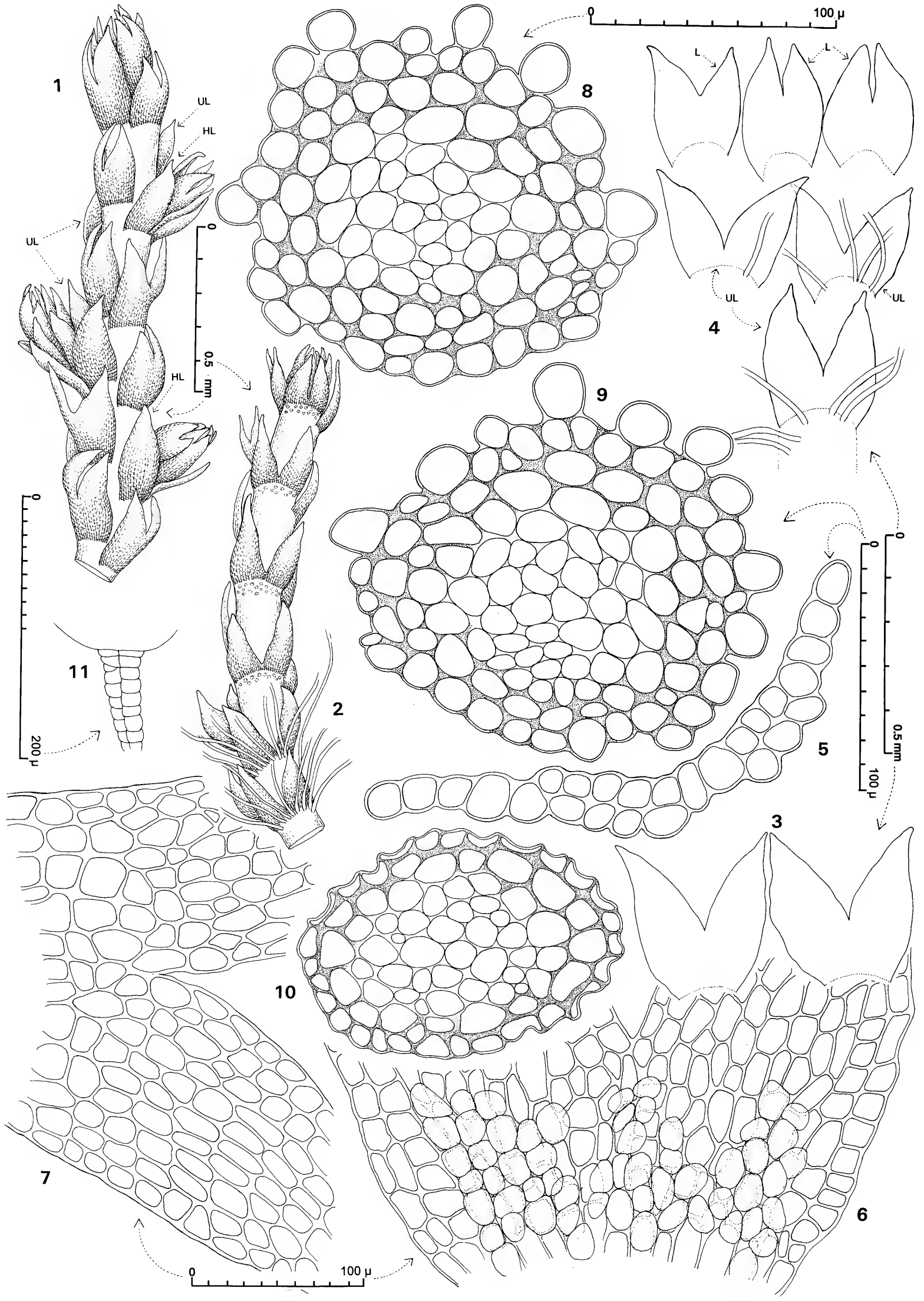

Fig. 125.
Anthelia juratzkana (Limpr.) Trevis. 1. Portion of shoot with 3 short *Frullania*-type branches, dorsal-lateral view (HL = half-leaf, at left not indicated; UL = underleaf). 2. Portion of shoot, the rhi-

branches per axis to rather freely pinnate, the branches of the *Frullania* type, often short; ventral-intercalary branches rare, microphyllous, stoloniform. Stems with dorsal and lateral sides with low, irregular, lamella-like ridges or strips of cells, the strips of cells contiguous with accessory cells on the abaxial surface of the leaf base, the stem in cross section with exposed wall of the hyaloderm cells notably thin, hyaline, bulging, often irregular in size and bubble-like, eventually collapsing with age, the subepidermal cells in 1–2 layers of thick-walled, pigmented cells, grading into a medulla of thin-walled cells. Rhizoids common, from stem in a rather broad zone at base of underleaf, wide for plant size, stiff. Leaves usually densely imbricate, concave to subcanaliculate, the insertion transverse but at times feebly succubous on laxer shoots, unistratose or locally bistratose in basal sector and then the leaf lamina crenulate in profile, the leaves elliptic to cuneate-quadrate, 200–325 μm wide × 240–350 μm long, bifid to 0.5–0.7; lobes erect, plane or feebly sulcate, narrowly acute, often apiculate, 8–14 cells wide at base, terminating in a single cell or a uniseriate row of 2 cells; lamina margins entire or feebly crenulate with slightly projecting shoulders of marginal cells. Cells moderately firm-walled, the marginal cells for the most part quadrate to short-rectangular, the cells of lobe base 13–17 μm wide × 20–25 μm long; surface smooth. Oil-bodies lacking. Underleaves virtually indistinguishable from leaves, except bilobed nearly to the base (the lamina 1–3 cells high) and with rhizoids at base. Fungal partner absent.

Paroecious. Gametangia terminal on leading shoots or on lateral branches, initially clavate or capitate, the densely imbricate bracts and bracteoles in several series, leaf-like, larger, bilobed to at least 0.5, the decolorate lobes and margins crenulate to serrulate-crenulate with projecting cells. Perianth short-ovoid, deeply lobed, the lobes serrulate-denticulate, almost included up to time of capsule dehiscence, closely sheathed by the erect, involute bracts.

Capsule (Schuster, 1974a) with outer layer of cells subquadrate or short-oblong, with 1–2(3) nodose thickenings on the longer walls, (0)1–2 on shorter walls, toward capsule base the epidermal cells more irregular, elongated, with sheet-like thickenings on longer walls, only locally nodular; inner layer of cells with narrowly rectangular, incomplete or weakly defined semiannular bands.

Spores delicately papillose, (15)16–18(20) μm in diam. Elaters 7–8.5 μm wide, with 2 or 3 narrow spirals.

Distribution and Ecology: Cosmopolitan in alpine and Arctic regions, southward to Spain, northern Italy, central Japan, Colorado and other montane areas at similar latitudes; disjunct in alpine areas from Mexico to Venezuela, Ecuador and Bolivia, to Tierra del Fuego, South Georgia, South Orkney Islands, South Shetland Islands, Livingston Island (Bednarek-Ochyra et al., 2000); also from Japan to Indonesia to alpine New Guinea, where it occurs at 3475–

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zoids shown at bases of 2 lower underleaves, their position indicated elsewhere, ventral view. 3. Two leaves. 4. Three leaves (= L) and 3 underleaves (= UL, with rhizoids indicated), all from same shoot. 5. Cross section through leaf base; note bistratose sector. 6. Basal sector of leaf showing bistratose area, abaxial aspect. 7. Basal sector of underleaf. 8, 9. Stem, cross sections through distal sector of shoot. 10. Stem, cross sections through lower sector of shoot; note collapse of hyaloderm cells (drawn to same scale as figs. 8, 9). 11. Antheridial stalk. (Figs. 1, 2, 4, 7, 10, 11, from *Engel 17883*, New Zealand, South Is., Westland–Otago EP boundary, Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton; 3, 5, 6, 8, 9, from *Engel 22053*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, area immediately below summit of Avalanche Peak.)

3500 m (Schuster, 1968b, 1974a) and to alpine areas of New Zealand. Also in Tanzania (Ochyra and Pócs, 1992). In New Zealand: South Island (1260–1900 m), North Island (1715–1790 m). Known from Fiordland (Mt. Burns), Otago (Old Man Ra., Dunstan Mtns., Aspiring Natl. Park), Westland (Galena Ridge), Canterbury (Mt. Taylor, Arthur's Pass), Western Nelson (Mt. Arthur) and Volcanic Plateau (Mt. Ruapehu) EPs. It is most frequent in central and western Otago and appears to be absent from the high mountains of Marlborough.

In New Zealand with the identical ecology seen in all other regions: usually on raw soil, often frost-heaved, in shallow valleys where snow lies late into the summer. At Avalanche Peak (Scotts Track, Arthur's Pass Natl. Park, 1650 m) plants occurred over a thick soil layer between boulders in the alpine zone. On the Young Ra. (Aspiring Natl. Park, 1900 m) it occurred on a flat soil terrace that has late snow lie, in *Poa colensoi* grassland with *Raoulia grandiflora*, *Gentianella divisa* and *Zotovia colensoi*. Also in penalpine scrub consisting mainly of *Chionochloa*, *Dracophyllum* and *Hebe* (below and W of Mt. Shrimpton, Mt. Aspiring Natl. Park, 1370–1470 m); at this station plants occurred over bare soil with *Diplophyllum*. On the summit of Mt. Arthur (Nelson, 1795 m) it is on the walls of a sinkhole, associated with *Poa colensoi*, *Luzula colensoi* and *Chionohebe pulvinaris*. On Mt. Ruapehu (vicinity of Turoa ski area, near SE Basin, Tongariro Natl. Park, ca. 1715–1790 m) the species occurs as scattered colonies on bare, dry soil of raised rocky soil beds that are between a seepage area and a stream in an area with alpine cushion vegetation. Commonly associated with *Andreaea* sp., *Cephaloziella* sp., *Conostomum pusillum*, *Dicranum aucklandicum*, *Herzogobryum teres*, *Nothogymnomitrion erosum*, *Notoligotrichum australe* and *Pachyschistochila nivicola*.

Comments: We have seen only the whitish, dwarfed phenotypes in New Zealand, and these occur in small patches, usually over bare soil, but the shoots, when creeping amidst other bryophytes and with crowding, sometimes may become erect. Although very small (the main stems only 3–6 mm long), the plants are in many cases rather freely pinnately branched, with branches all of the *Frullania* type (Fig. 125: 1). The plants have the usual strongly water-repellent, whitish, light-reflecting surface so typical of the genus as a whole. Schuster (1974a, p. 639) states "plants of *A. juratzkana* are often somewhat covered by a pruinose or whitish secretion, consisting of crystalline filaments or needles (*teste* Müller, 1951–58), which is not a fungus, although it has been considered to be of fungal origin. However, in the living plant, at least, it appears to be in the form of a thin, opaque, whitish layer which renders the plants nearly waterproof..." Plants can be easily overlooked as a whitish crustose lichen.

The stem anatomy is noteworthy. The dorsal and lateral sides of the stem have low, irregular, lamella-like ridges or strips of cells. The strips of cells are contiguous with those on the abaxial surface of the leaf lamina, i.e., below the level of the sinus. The strips of cells are best observed in the distal sector of the shoot and are less conspicuous on older, lower, pigmented sectors. In stem cross section the strips of cells may be seen as bulging, often irregular, often huge cells accessory to the hyaloderm cells (Fig. 125: 8, 9). On lower, pigmented sectors of the shoot the exposed wall of the hyaloderm cells for the most part collapses toward the cell interior and the accessory cells have been sloughed off. The thickened radial and inner tangential walls of the cortical cells remain, lending an irregular surface to the stem (Fig. 125: 10).

The leaf lamina is often locally bistratose (Fig. 125: 5, cross section). The accessory cells occur in an irregular field on the abaxial surface and are bulging and hemispherical vs. the elongate cells of the lamina (Fig. 125: 6, surface view of field). The hemispherical cells lend the leaf lamina a distinctly crenulate profile.

The populations from the Antarctic Peninsula differ from both the New Zealand represen-

tatives and those of the Northern Hemisphere by having a "hyaloderm of firm-walled cells" (Bednarek-Ochyra et al., 2000, p. 97) that are thickened even on the exposed face of the cells (Bednarek-Ochyra et al., 2000, fig. 42: 11). The hyaloderm of New Zealand plants consists of cells that are very thin-walled, at least on the outer tangential wall (Fig. 125: 8, 9). Also, epidermal cells of the stem are regular in size and shape and do not bulge in the Antarctic populations (Bednarek-Ochyra et al., 2000, fig. 42: 11). In the New Zealand populations the strips and ridges of cells on the stem are seen in stem cross section as thin-walled, accessory cells that are irregular in size and shape, and freely bulge (Fig. 125: 8, 9). The hyaloderm cells in Northern Hemisphere populations are regular in shape and distinctly bulge (Schuster, 2000a, fig. 52: 2). The underleaves of the Antarctic populations are more shallowly divided than in New Zealand plants (compare fig. 42: 2, 6, 7 in Bednarek-Ochyra et al. [2000] with Fig. 125: 2, 4). Schuster (1974a) illustrated underleaves from North American material and showed one underleaf with a distinct lamina (fig. 434: 8) and another with a lamina 4 cells high (fig. 435: 5).

Suborder 7. **CEPHALOZIINEAE** R.M.Schust.

Jungermanniales suborder *Cephaloziineae* R.M.Schust., J. Hattori Bot. Lab. 36: 391. 1972.

Although the suborder has many representatives in the Northern Hemisphere, all of the families occur in the Austral areas. Four families are included in the *Cephaloziineae*: *Cephaloziaceae*, *Cephaloziellaceae* and *Adelanthaceae*, which are well-represented in our area, and the *Jackiellaceae*, which is represented only by a single species in New Zealand.

Family **CEPHALOZIACEAE** Mig.

Cephaloziaceae Mig., Krypt.-Fl. Deutschland 1: 465. 1904.

Plants predominantly markedly anisophyllous, rarely subisophyllous (*Hygrobiella*), often soft-textured and/or lax, usually creeping in growth but sometimes with ascending gemma-bearing axes (lacking in ours), often green, hyaline, the exposed sectors often with reddish, purplish, brownish or fuscous pigments, small to medium in size. Branching sparing and irregular, the branches for the most part ventral-intercalary; lateral-intercalary branches present in some taxa; *Frullania*-type terminal branching in a few taxa; *Andrewsianthus* type present in *Odontoschismatoideae*; stolons and flagelliform axes often developed. Stems various, the cortical cells often larger than medullary cells, at times forming a distinct hyaloderm, at times thick-walled. Rhizoids hyaline to pale brown, scattered, at times rather dense. Leaves alternate, bifid (in ours; 3[4]-lobed in *Cephalozia chilensis*) to bidentate (*Alobiella*) to unlobed, the insertion mostly succubous, at times nearly transverse, not extending to stem midline dorsally and delimiting a leaf strip (extending to stem midline in *Metahygrobiella*). Cells thin-walled to, less often, firm-walled (excluding *Odontoschismatoideae*), mostly devoid of trigones; surface smooth. Oil-bodies generally (always in ours) lacking, small and granular in a few taxa, large in *Odontoschismatoideae*. Underleaves bilobed, small to vestigial and then reduced to slime papillae or to a small scale-like lamella bearing slime papillae (the underleaves subequal to leaves in *Hygrobiella*). Asexual reproduction frequent, often via 1(2)-celled gemmae produced from reduced leaves of tapered branches.

Dioecious, often autoecious, rarely paroecious. Androecia usually on short, ventral-intercalary branches, less frequently on leading shoots, typically spicate; bracts usually much smaller than

leaves, usually bilobed, concave at base to strongly ventricose; antheridia normally 1 per bract, the jacket-cells elongated, tiered (except *Odontoschismatoideae* and *Schiffneria*), the stalk 2-seriate; bracteoles, when present, lacking antheridia. Gynoecia isophyllous, at apices of weak ventral-intercalary branches, less often terminating long leafy axes; bracts in 1–3 series, nearly uniformly bifid; bracteoles free from bracts, identical to bracts or nearly so. Perianth well developed, terete below, bluntly trigonous distally, with 2 keels lateral + 1 ventral, the dorsal face flat; perianth usually unistratose but at times with up to 8 strata below. Coelocaule absent. Calyptra thin, never fleshy.

Foot lacking a well-developed haustorial collar. Seta usually with 8(9) rows of outer cells and 4(5) rows of internal cells. Capsule wall 2–3-stratose; outer layer of cells normally oblong, with two-phase development, the alternating walls with nodular to nodular-confluent thickenings, or (*Metahygrobiella*) with two-phase ontogeny indistinct.

Spores papillose to papillose-vermiculate or (*Schiffneria*) areolate.

There are 16 genera in the family, which is worldwide in distribution. The family is well represented in the Neotropics, with nine genera occurring there (Gradstein et al., 2001). The *Cephaloziaceae* include six subfamilies, only one of which (subfam. *Cephalozioideae*) occurs in New Zealand and is represented only by a few species in two genera (*Metahygrobiella*, *Cephalozia*). The other genera in subfam. *Cephalozioideae* are *Cladopodiella* Buch (two species), *Nowellia* Mitt. (10 species), *Pleurocladula* Grolle (one species) and *Schofieldia* J.D.Godfrey (one species). The other five subfamilies do not occur regionally and are as follows.

1) subfam. *Alobielloideae* R.M.Schust. has three genera, one, *Alobiellopsis* R.M.Schust., with five species, two represented in South Africa (*A. heteromorphus* (Lehm.) R.M.Schust., *A. pillansii* (Sim) R.M.Schust.); the other two genera are *Alobiella* (Spruce) Schiffn. (monotypic) and *Iwatsukia* N.Kitag. (four species).
2) subfam. *Hygrobielloideae* R.M.Schust. has one genus, *Hygrobiella* Spruce, which is monotypic and is subarctic to low arctic in distribution.
3) subfam. *Odontoschismatoideae* Buch *ex* Grolle, with two genera, *Odontoschisma* (Dumort.) Dumort. (ca. 12 species) and *Anomoclada* Spruce (monotypic).
4) subfam. *Schiffnerioideae* R.M.Schust., with only *Schiffneria* Steph.
5) subfam. *Trabacelluloideae* (Fulford) R.M.Schust. with only the monotypic *Trabacellula* Fulford. Schuster (2002a) also included *Fuscocephaloziopsis* Fulford (two species) and *Haesselia* Grolle & Gradst. (two species) in this subfamily, but Engel and Braggins (2005) showed that further studies are required prior to a decision as to subfamily placement of the last two genera. Note that Gradstein et al. (2001) regard *Fuscocephaloziopsis* as a synonym of *Cephalozia* subg. *Macrocephalozia*.

Separation of genera and subgenera at times may be difficult within our area, and a separate key is included, as follows.

Key to Genera and Subgenera

1a. Leaves inserted to (or nearly to) stem midline, the line of insertion at least in dorsal third nearly or quite transverse; leaves strongly concave, sometimes concave-conduplicate; plants usually with reddish or brownish pigments. Gemmae always lacking; gynoecia usually on long leafy axes 2

2a. Leaves mostly clearly elongated, at least loosely canaliculate or conduplicate; leaf insertion strictly transverse dorsally (except sometimes in *M. drucei*), the leaves vertically oriented and with the concavity oriented toward shoot apex; lateral-intercalary branches in some extraterritorial taxa . . . . . *Metahygrobiella*

2b. Leaves usually as wide as long or wider, strongly concave to hemispherical; leaf insertion somewhat succubous dorsally, the leaves succubously oriented, the concavity not turned to shoot apex; lateral-intercalary branches completely lacking, the branches either all ventral-intercalary or in part *Frullania* type . . . . . *Cephalozia* subg. *Eocephalozia*

1b. Leaves leaving all or almost all of dorsal two rows of cortical cells leaf-free, the insertion distinctly succubous; leaves usually shallowly concave, the concavity (leaf surface) turned upward; plants usually not pigmented. Gemmae often present; gynoecia often on short, abbreviated branches . . . . . *Cephalozia*

Metahygrobiella R.M.Schust.

Metahygrobiella R.M.Schust., Bryologist 64: 205. 1961.

Plants usually soft and flaccid, for the most part pellucid, whitish to locally brownish or purplish in some taxa, the shoots sometimes becoming flagelliform, but geotropic, rhizoidous, flagelliform axes lacking. Stems soft, the cortical cells thin to weakly thick-walled, usually larger than medullary. Rhizoids often sparse, scattered. Branching sparing to common, the branches of the *Frullania* type in some taxa; ventral-intercalary and/or lateral-intercalary branches present in some taxa. Leaves remote to contiguous, rarely imbricate, transversely to subtransversely oriented, the insertion transverse at least in dorsal sector but at times (*Metahygrobiella drucei*) distinctly succubous below, the insertion lines extending to stem midline dorsally; leaves concave to concave-conduplicate, the concavity oriented toward shoot apex, bifid to 0.35–0.55; lobes acute to subacuminate, the apices at times filiform. Cells lax, subhyaline, weakly chlorophyllose, thin-walled, trigones absent, the cells large, those above to 40 μm × 70 μm. Oil-bodies lacking or with numerous, hyaline, minute (ca. 1 μm in diam.) oil-droplets. Underleaves absent (at times locally present in *M. drucei*). Asexual reproduction lacking or (*M. mollusca*) by 1-celled greenish gemmae at tips of erect shoots.

Dioecious. Androecia terminal but eventually becoming intercalary on elongated, leafy axes, laxly spicate; bracts leaf-like but bases more concave, the lobes erect; antheridia 1(2) per bract, the stalk 2-seriate; bracteoles lacking. Gynoecia on long, leafy axes; bracts and bracteoles bifid, the margins usually entire. Perianth long-tubular, trigonous distally, the mouth crenulate varying to laciniate; perianth (1)2(3)-stratose toward base.

Seta of the 8+4(5) type, the inner cells not much smaller. Capsule short- to long-ellipsoidal, the wall bistratose; outer layer of cells usually tiered, oblong, without obvious two-phase ontogeny: all or nearly all longitudinal walls with sinuous-nodular, confluent thickenings; inner layer of cells with well-developed semiannular bands.

Spores with close papillae and short-vermiculate markings or tuberculate-vermiculate; spore:elater diam. ratio 1.4–1.8:1. Elaters rather rigid, at most only moderately tortuous, bispiral to the tips.

Type: *Metahygrobiella acuminata* (Herzog) R.M.Schust. (≡ *Hygrobiella acuminata* Herzog)

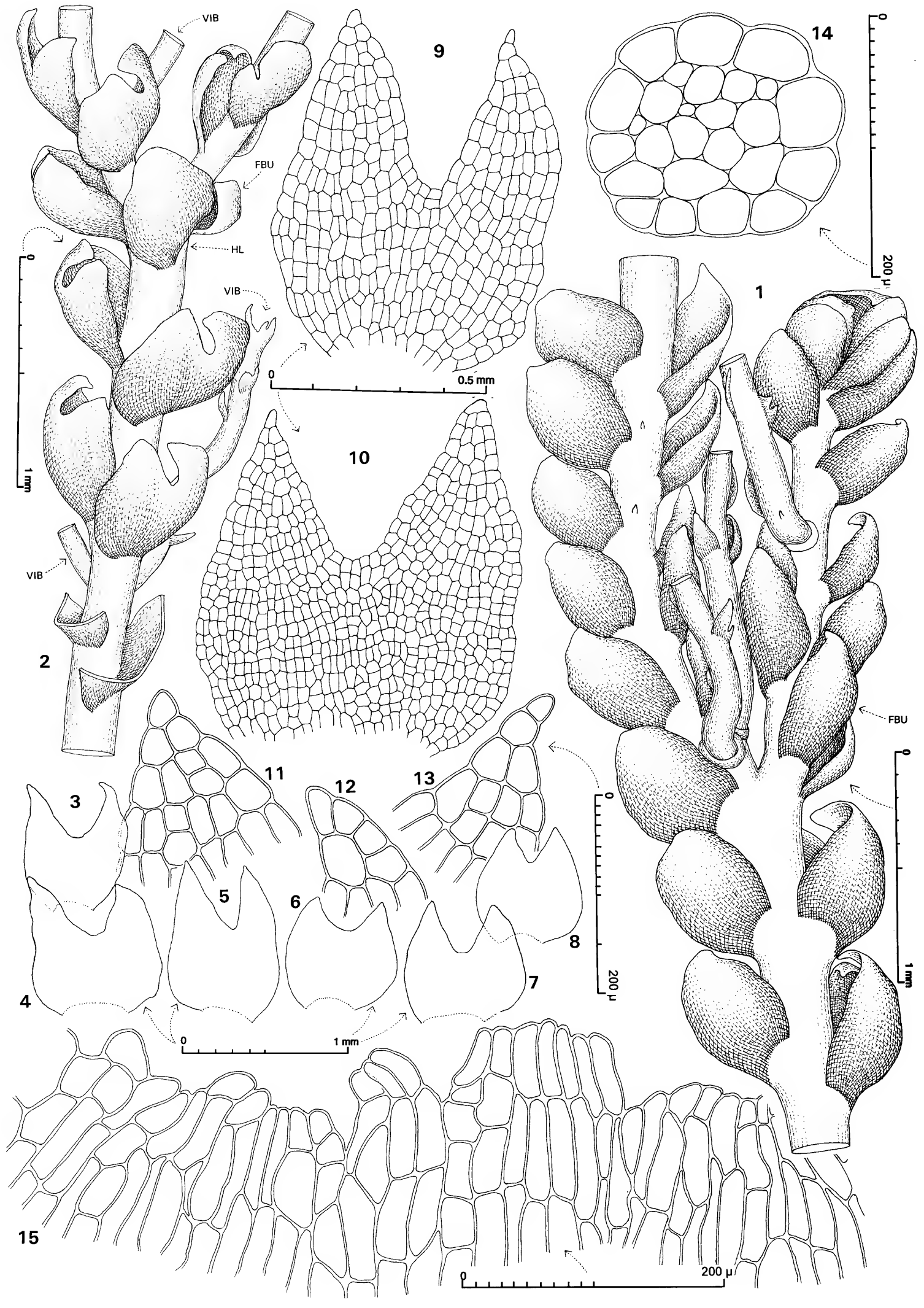

Fig. 126.
Metahygrobiella drucei R.M.Schust. 1. Portion of shoot with *Frullania*-type branch (FBU = first branch underleaf) and 3 ventral-intercalary branches (ventral view); note several minute underleaves. 2. Portion of shoot (dorsal aspect) with *Frullania*-type branch (HL = half-leaf; FBU = first

A genus of ca. 10 species, most occurring in tropical sectors of the old world. The genus occurs in New Guinea (three species), Borneo (three species), the Philippines, Amboina, Malaya, southern Japan (Kyushu), the Himalayas (*Metahygrobiella albula* (Steph.) Grolle) and Hawaii (*M. lucens* (A.Evans) H.A.Mill.). Two species occur in the south temperate zone: *M. tubulata* (Hook.f. & Taylor) R.M.Schust. *ex* J.J.Engel of southern South America and the Falkland Islands (Engel, 1978, 1990a) and *M. drucei* from our area. *Metahygrobiella monoica* E.A.Hodgs. of New Zealand was transferred to *Lophozia*, as *Lophozia monoica* (E.A.Hodgs.) J.J.Engel.

References: Schuster (1964a, 2002a).

Metahygrobiella drucei R.M.Schust.

[Figs. 126, 127; Fig. 128: 1, oil-bodies, p. 558]

Metahygrobiella drucei R.M.Schust., J. Hattori Bot. Lab. 26: 273. 1963. Holotype: New Zealand, North Is., Mt. Hector, West Peak, 4500 ft., *Schuster 60444* (F).

Metahygrobiella tayloriae E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 75. 1965, *syn. fide* Schuster (1969a, p. 65). Holotype: New Zealand, South Is., Fiordland, Key Summit, 15 Dec. 1962, *MacMillan, Morice & Taylor* (herb. Hodgson no. 12634) (MPN!); isotype: (CHR – *absens*).

Metahygrobiella cylindrica E.A.Hodgs. & Herzog *in* E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 189. *f. 4, A–F*. 1967, *syn. fide* Schuster (2002a). Holotype: New Zealand, North Is., Tararua Mtns., N face of Mt. Hector, ca. 4300 ft., *Zotov s.n.* (CHR no. 7492!); isotype: (MPN, Hodgson herb. no. 477, *non vidi*).

Plants flaccid, very soft-textured and spongy, hyaline and whitish below, the distal parts of leaves, bracts and perianths reddish to purplish, intense purplish in sun forms, medium, to 1000 μm wide. Stems hyaline, with a rather well-defined hyaloderm, the medullary cells thin-walled. Rhizoids not seen. Branching common, the branches of the *Frullania* type, often several per shoot; ventral-intercalary commonly present, leafy or at times initially stoloniform but ultimately becoming leafy, the collar low, rather broad. Leaves contiguous to weakly imbricate, subtransversely oriented, the insertion transverse or subtransverse to weakly succubous in dorsal third, but with remainder of insertion distinctly succubous, the leaves concave, often deeply so, often appearing inflated and billowed out, orbicular-subquadrate to subrectangular, *in situ* flaring dorsally and partially overlapping dorsal sector of opposing leaf, 500–870 μm wide × 700–1100 μm long, symmetrically bilobed to (0.25)0.3–0.5; lobes often sharply incurved, subequal, medium acute, terminating in a single cell or a uniseriate row of at most 2 cells, the tip cell at most slightly longer than wide, the lobes 9–16 cells wide at base, the lobe

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branch underleaf) and 3 ventral-intercalary branches (= VIB); note that leaf insertions extend to stem midline dorsally and that the lowermost insertion is oblique at dorsal end while the insertion of the leaf immediately above is transverse at dorsal end. 3–8. Leaves, all drawn to same scale. 9, 10. Leaves (note differences in areolation). 11–13. Leaf lobes, all drawn to same scale. 14. Stem, cross section. 15. Perianth mouth. (Figs. 1, 2, 6–8, 10, 14, 15, from *Engel 17730*, New Zealand, South Is., Otago EP, summit plateau of Mt. Maungatua, 825 m; 3–5, 9, 11–13, from *Engel 24990*, New Zealand, South Is., Western Nelson EP, Mt. Arthur, Horseshoe Basin, near Tableland Track via Gordons Pyramid, ca. 1400 m.)

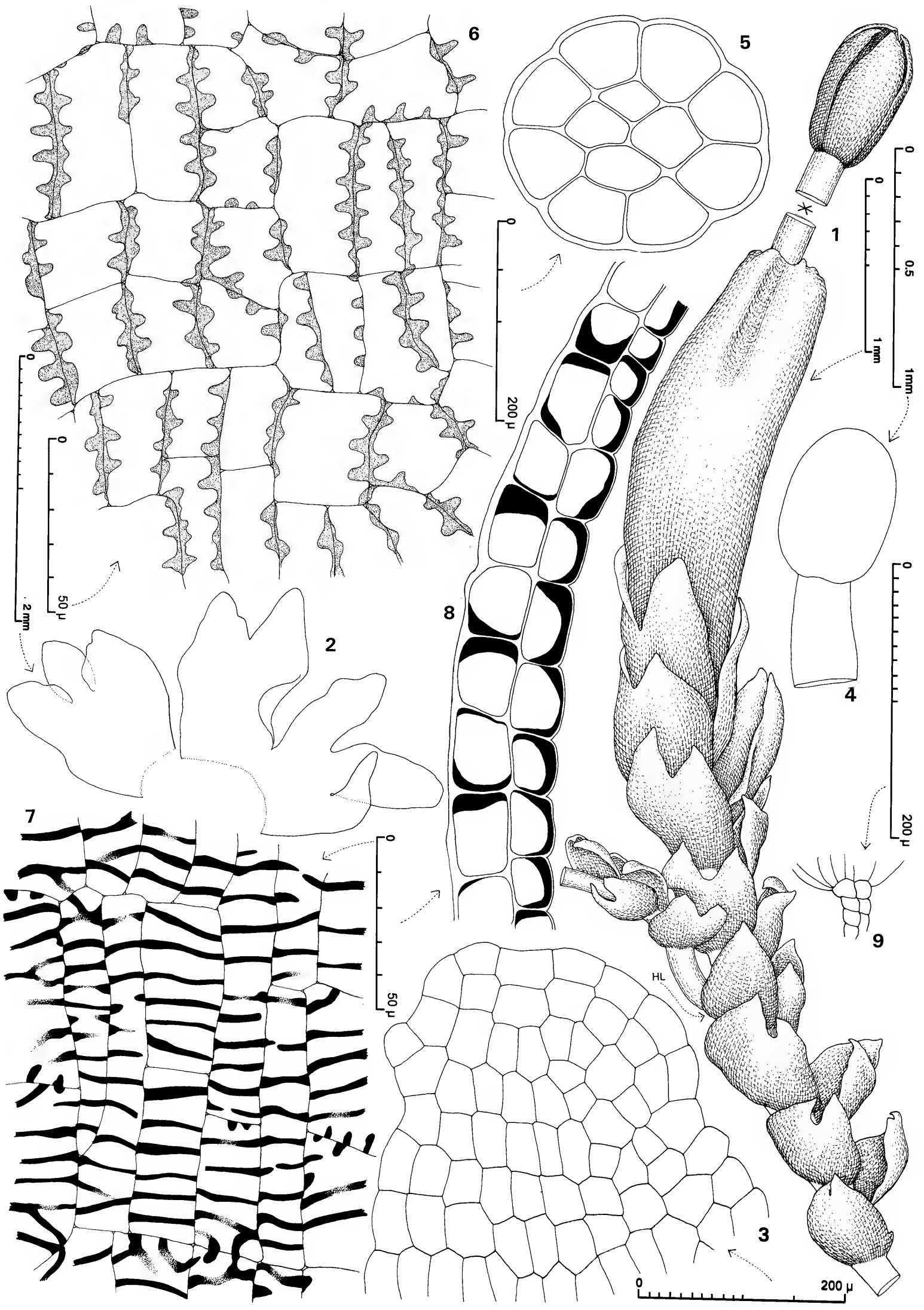

Fig. 127.
Metahygrobiella drucei R.M.Schust. 1. Leading shoot with gynoecium and mature sporophyte + a *Frullania*-type branch (HL = half-leaf), dorsal-lateral view. 2. ♀ Bracts and, in middle, bracteole. 3. Lobe of ♀ bract. 4. Seta and capsule profile. 5. Seta, cross section. 6. Capsule wall, outer

margins entire. Cells in median sector of lamina with walls very thin, completely devoid of trigones, 19–29 μm wide × 28–43 μm long to 24–36 μm wide × 50–60(80) μm long, the cells of lobes in regular tiers. Oil-bodies lacking or with numerous, hyaline, minute (ca. 1 μm in diam.) oil-droplets. Underleaves absent but at times locally present and then of a few cells (e.g., biseriate at base + single cell capped by a slime papilla), at times distinct, wider than the stem and ovate to elliptic, undivided and entire. Asexual reproduction lacking. Fungal partner an ascomycete.

Dioecious. Androecia terminal but eventually becoming intercalary on elongated, leafy axes, subfoliose; bracts similar to leaves except somewhat more closely imbricate, with bases more concave and the lobes erect; antheridia 1 per bract, the stalk 2-seriate; bracteoles lacking. Gynoecia terminal on long or leading leafy axes; bracts and bracteoles in 3 series, the bracteoles of first series subquadrate and with a retuse apex, those of second series large, obovate, with apex retuse to irregularly bilobed; bracts much larger than the leaves, free dorsally, rather sharply and irregularly longitudinally undulate, 3-lobed, the lobes blunt to narrowly rounded at the summit, the lobe and lamina margins entire; bracteoles similar in size to bracts, free or distinctly connate on one side and free on the other, the apices bilobed, the lobes similar to those of the bracts. Perianth rather long, elliptic to subfusciform, cylindrical below, trigonous above (often distinctly so), with 2 keels lateral + 1 ventral, narrowed to the contracted mouth; mouth crenulate but with some sectors entire and straight, without suggestion of protruding free ends of cells; perianth 1–2-stratose toward base.

Seta of the 8 rows of outer cells and 4(5) rows of inner, somewhat smaller cells. Capsule short-ellipsoidal, the wall 2(very locally 3)-stratose, 35–36 μm thick; outer layer of cells tiered, subrectangular, but becoming quadrate with occasional secondary transverse cell wall divisions, with two-phase ontogeny obscure: all or most longitudinal walls with continuous sheets of secondary, pigmented wall material and frequent nodules, lending the walls a sinuous appearance, the alternating longitudinal walls at times with thickenings less well developed (but rarely altogether absent) and then with a suggestion of two-phase development; inner layer of cells with semiannular bands well developed, usually complete, the bands rather closely spaced, narrow, sporadically forked, particularly at the cell ends.

Spores 13–15.4 μm in diam., with low but distinct, close papillae and short-vermiculate markings; spore:elater diam. ratio 1.4–1.8:1. Elaters rather rigid, at most only moderately tortuous, 8.6–9.6 μm wide, tapering to ends, bispiral to the tips, the spirals 2.9–3.4 μm wide, closely wound.

Distribution and Ecology: Endemic to New Zealand: South Island ([825]920–1500 m).

A helophyte, occurring in penalpine and alpine areas over peaty soil in saturated or near-saturated conditions associated with pools, tarns and ponds, often associated with *Sphagnum*. On the summit plateau of Mt. Maungatua (30 km W of Dunedin) occurring over saturated peaty soil at pool margins in an area of tussock grassland with mosaic of scattered bogs having abundant *Sphagnum* and patches of *Dracophyllum*, *Halocarpus bidwillii*, *Hebe odora* and *Donatia novae-zelandiae*. Also at the margin of a still, small pond at ca. 1500 m in communities of penalpine shrubs and cushion vegetation, rocky herbfields and *Dracophyllum* (Horse-

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layer. 7. Capsule wall, inner layer. 8. Capsule wall, cross section. 9. Antheridial stalk. (Figs. 1–8, from *Engel 17730*, New Zealand, South Is., Otago EP, summit plateau of Mt. Maungatua, 825 m; 9, from *Child 3835*, New Zealand, South Is., Otago EP, Lammermoor Ra., ca. 760 m.)

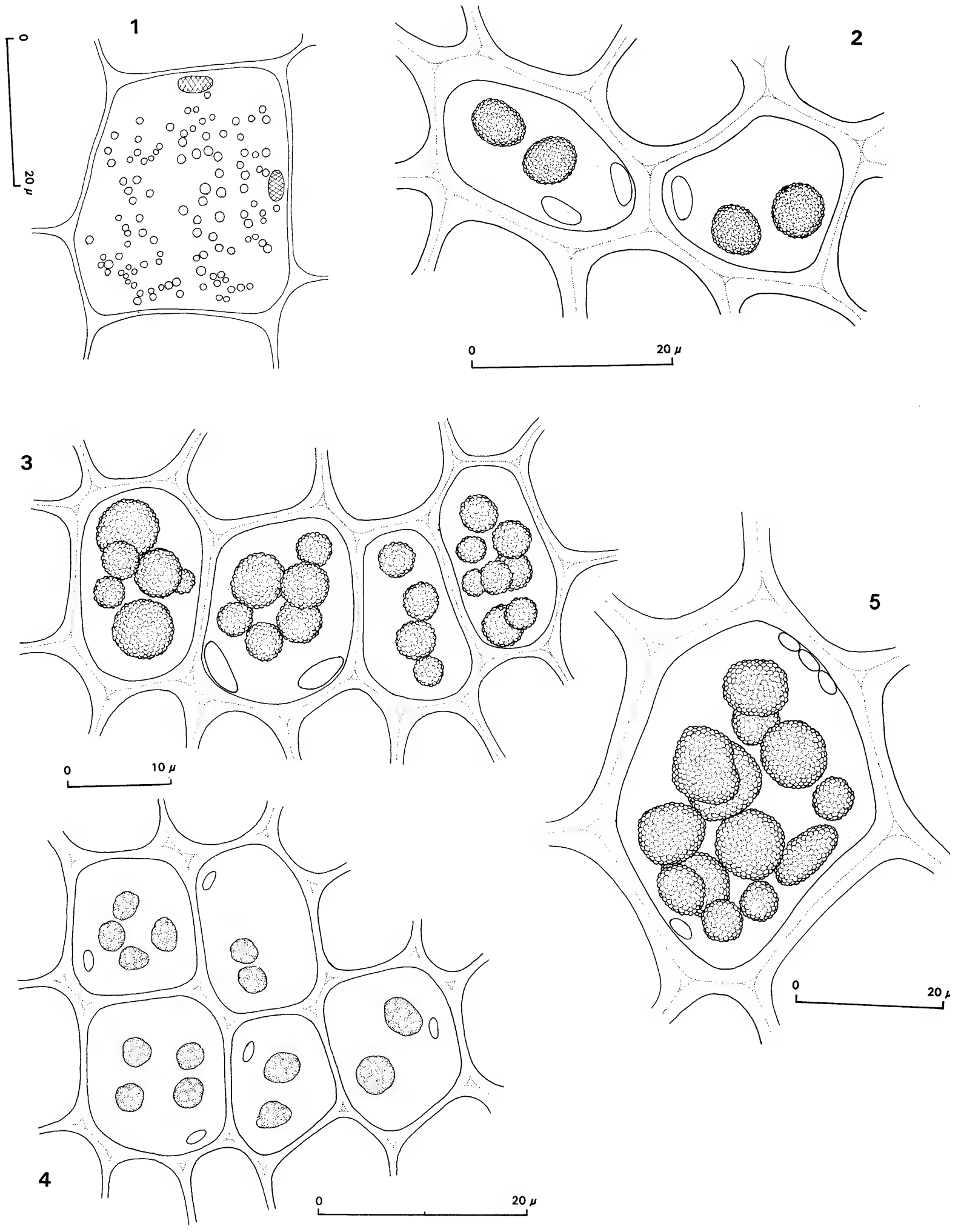

Fig. 128.
Oil-bodies, all (except fig. 1) with the outline of a few chloroplasts included. 1. *Metahygrobiella drucei* R.M.Schust. Leaf cells showing "Schrot-Korn" type of oil-bodies. 2. *Allisoniella nigra* subsp. *nigra* var. *acutiloba* J.J.Engel. Median leaf cells. 3. *Cephalomitrion aterrimum* (Steph.) R.M.Schust. Median disc cells. 4. *Cephaloziella pseudocrassigyna* R.M.Schust. *ex* J.J.Engel. Cells at base of lobe. 5. *Pseudomarsupidium piliferum* (Steph.) Herzog *ex* Grolle. Median leaf cells. (Fig. 1, from *Glenny 8922*, New Zealand, South Is., Canterbury EP, Arthur's Pass, Margaret Tarns track;

shoe Basin, Mt. Arthur, Kahurangi Natl. Park). In the alpine zone, for example, at the edge of a tarn with *Sphagnum* in a mosaic of tussockland and alpine vegetation along with tarns, rills, rocky outcrops and boulderfields (Rainbow Skifield, St. Arnaud Ra., Nelson Lakes Natl. Park, 1360–1480 m). Plants often form very lax, soft, stringy mats, and at times may be submerged, at least after snow melt and after rains.

Comments: *Metahygrobiella drucei* has somewhat the aspect of a *Cephalozia*, but the dorsal end of the leaf insertion is transverse and the leaves are more concave, with longer, drawn-out leaf lobes. Plants are characteristically hyaline and whitish below, but the distal parts of leaves, bracts and perianths have a reddish to purplish coloration.

The type of *Metahygrobiella cylindrica* has leaves that are distinctly succubous on sterile shoots, the angle of insertion being less than 45° to the stem axis. However, the leaves just below the gynoecium are more imbricate and subtransverse. The underleaves are distinct and obvious below the gynoecium.

Cephalozia (Dumort.) Dumort.

Jungermannia sect. *Cephalozia* Dumort., Syll. Jungerm. Europ. 60. 1831. *Cephalozia* (Dumort.) Dumort., Recueil Observ. Jungerm. 18. 1835.

Plants rather pellucid, typically soft-textured, usually creeping and adhering to substrate, mostly pale or yellowish green, at times with intense reddish to brownish pigments, small to very small, to 1200 μm wide. Branching irregular, often sparingly, the branches of the *Frullania* and ventral-intercalary types; stoloniform, geotropic, ventral-intercalary branches present in many taxa. Stems soft-textured, with cortex in a single layer of usually 10–12(16) rows of large, often thin-walled cells; medullary cells in 6 to many rows, small, usually weakly to moderately thick-walled. Rhizoids copious, scattered. Leaves usually remote to contiguous, rarely imbricate, the insertion somewhat to strongly succubous throughout, the insertion lines usually leaving at least 2 rows of dorsal cortical cells leaf-free (the lines of insertion approaching stem midline in subg. *Eocephalozia*); leaves usually shallowly concave, the concavity (leaf surface) turned upward, ovate to rotund, usually rather few-celled, 0.25–0.5(0.65–0.75) bifid, the sinus, at least at base, usually rounded, the lobes straight or connivent, acute to subacute, sharp, the lobe margins entire; lamina margins entire, the ventral never developing a gibbous water sac. Cells mostly thin-walled, exceptionally slightly and evenly thick-walled, lacking trigones, usually rather large (most 24–45 μm in diam.), pellucid; surface smooth. Oil-bodies absent. Underleaves reduced to ephemeral slime papillae, or rarely, small and scale-like. Asexual reproduction often present, by 1-celled, spherical or ovoid, greenish (never pigmented) gemmae produced on erect, attenuated axes.

Dioecious or autoecious, rarely paroecious or heteroecious. Androecia on main shoot or short to long ventral-intercalary branches (occasionally on lateral-intercalary branches in *Cephalozia badia*), the androecia terminal but usually becoming intercalary, laxly spicate;

2, from *Glenny 9317*, type; 3, from *Glenny 9200*, New Zealand, South Is., Westland, Upper Otira Valley; 4, from *Engel 27333*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Bealey Valley Track; 5, from *Glenny 9727*, New Zealand, South Is., Canterbury EP, Arthur's Pass, Bealey Chasm.)

bracts bilobed, the dorsal base often with a discrete, incurved tooth or lobe; antheridia 1 per bract. Gynoecia long, leafy shoots or short, abbreviated intercalary branches; bracts in 2–4 progressively larger series, concave, usually bifid but with elaboration of lateral teeth sometimes 4-fid; bracteoles similar to bracts, often connate at base with one or both bracts. Perianth long-emergent, not subtended by a perigynium, terete basally, bluntly trigonous above, gradually narrowed toward mouth; mouth crenulate to ciliate.

Seta usually of the 8+4 type. Capsule long-exserted, ellipsoid to ovoid, the wall bistratose; outer layer of cells with two-phase ontogeny, the alternating longitudinal walls with strong nodular thickenings; inner layer of cells with nodular to spur-like thickenings on radial walls, semiannular bands at times present, incomplete or complete.

Spores finely papillose; spore:elater diam. ratio 1:1. Elaters bispiral.

Type: *Cephalozia bicuspidata* (L.) Dumort. (≡ *Jungermannia bicuspidata* L.)

A genus of 26 species worldwide (cf. Váňa, 1988, p. 179). While the genus is more species rich in boreal–subarctic–Arctic areas than in south temperate areas, only one of the three subgenera occurs in Laurasian vs. two subgenera in Austral areas, including our area. For example, Schuster (1974a) treats 11 species for North America, all in subg. *Cephalozia*. Only three species occur in southern South America: *C. badia*, which also occurs in our area; *C. pleniceps* (Austin) Lindb., which is circumboreal + southern Chile = *Cephalozia patagonica* Fulford, Fulford, 1968a; *fide* Schuster, 1986); and *Cephalozia chilensis* (J.J.Engel & R.M.Schust.) R.M.Schust., Beih. Nova Hedwigia 119: 29. 2002 (≡ *Metahygrobiella chilensis* J.J.Engel & R.M.Schust., Brittonia 40: 203. 1988, *nom. nov. pro Cephalozia heteroica* R.M.Schust. & J.J.Engel, Fieldiana 41: 219. 1978, *non C. heteroica* Cooke [Cooke, 1904]). *Cephalozia cucullifolia* Steph., Wiss. Ergeb. Schwed. Südpolar-Exped. 1901–1903, 4(1): 8. 1905, described from the South Shetland Islands, is a synonym of *C. badia* (*fide* Grolle, 1972d). Váňa (1988) discussed and provided a key for African taxa. Wigginton and Grolle (1996) report three species from sub-Saharan Africa: *C. africana* Váňa, *C. bicuspidata* (L.) Dumort. and *C. fissa* Steph. The genus is represented in our area by four taxa.

The genus *Cephalozia* in New Zealand is relatively poorly understood and all of the species in this treatment require further investigation. The generic description was adapted, with considerable modification, from Schuster (2002a).

References: Schuster (1964a, 2002a).

Key to Species

1a. Leaf insertion extended virtually to stem midline dorsally; plants (in sun) brown to purplish, at least above; stem lacking a hyaloderm, the dorsal and lateral cortical cells not or little larger in diameter than the medullary cells; gemmae lacking; leaf lobes 5–14 cells wide at base; gynoecia usually or always on long leafy axes. Subg. *Eocephalozia* 2

2a. Stem cortical cells all thin-walled, in 13–15 rows; dioecious (?or autoecious). Leaves all bilobed . . . . . *C. badia* (p. 561)

2b. Stem cortical cells firm-walled, in 11–14 rows; autoecious 3

3a. Perianth mouth crenulate with little-elongated cells (to 2:1), never with a uniseriate row of 2 free cells, the perianth base 4–6-stratose; sterile shoots underleaf-free. . . . . *C. pachygyna* (p. 563)

3b. Perianth mouth ciliolate with numerous short, free teeth composed of (1)2–4 elongated cells (3.1–4.1:1), the base 1–2-stratose; sterile shoots locally with large underleaves . . . . . *C. schusteriana* (p. 563)

1b. Leaf insertion not extended to near stem midline, a continuous band of cortical cells leaf-free present; plants (in sun) intense vinaceous to carmine; stem with a hyaloderm, the dorsal and lateral cortical cells strongly inflated, much larger than medullary cells; gemmae present; leaf lobes 4–5 cells wide at base; gynoecia on axes of variable length, some on short ventral branches. Subg. *Cephalozia* . . . . . *C. austrigena* (p. 565)

Subg. ***Eocephalozia*** R.M.Schust. *ex* J.J.Engel

Cephalozia subg. *Eocephalozia* (R.M.Schust.) J.J.Engel, Novon 17: 312. 2007. Type: *Cephalozia badia* (Gottsche) Steph. (≡ *Jungermannia badia* Gottsche).

Cephalozia badia (Gottsche) Steph.

Jungermannia badia Gottsche, Ergebn. Deutsch. Polar-Exped. 2(16): 452. *pl. 1, f. 1–5*. 1890. *Lophozia badia* (Gottsche) Steph., Wiss. Ergeb. Schwed. Südpolar-Exped. 1901–1903, 4(1): 8. 1905. *Cephalozia badia* (Gottsche) Steph., Sp. Hepat. 3: 313. 1908. Type: South Georgia, Köppenberg, 10 Feb. 1883, *Will* (F!, slide ex herb. Schuster).

Cephalozia cucullifolia Steph., Wiss. Ergeb. Schwed. Südpolar-Exped. 1901–1903, 4(1): 2. *f. 1, 2*. 1905. Type: South Shetland Is., Nelson Is., Harmony Cove, 1902, *Skottsberg* (*syn. fide* Grolle, 1972d) (F!, ex herb. Schuster).

Cephalozia badia fo. *minor* Grolle, Bull. Brit. Antarct. Surv. 28: 83. 1972, *nom. nud.*, *syn. fide* Bednarek-Ochyra et al., 2000). Type: South Sandwich Is., Leskov Is., summit ridge, *Longston 501*.

Plants soft, slender, prostrate, procumbent or ascending, when in moss cushions then erect, the plants whitish green, with at least the distal parts of leaves, bracts and perianth apex brownish or fuscous or purplish brown, medium sized, the shoots to 500 μm wide. Branching sporadic to frequent, the branches typically of *Frullania* type, the half-leaf distinct, ovate; ventral-intercalary type branches also present, small-leaved. Stems with cortical cells in 13–15 rows, thin-walled, slightly to at most moderately larger than those of the medulla; medullary cells thin-walled. Rhizoids scattered, hyaline or brownish. Leaves vertically oriented, strongly dorsally assurgent, variably spreading, suberect to obliquely so, remote to contiguous, succubously to subtransversely oriented, the insertion obliquely succubous throughout to subtransverse, extending virtually to stem midline dorsally, the leaves moderately to strongly concave (cupulate), broadly ovate to suboblate, uniformly bilobed to 0.4–0.5; lobes usually incurved, erect, not connivent, not drawn out, the ventral often slightly larger, broadly subacute to acute, the apices often blunt, terminating in a single cell (or a pair of laterally juxtaposed cells) or, exceptionally, a uniseriate row of 2(3) cells at most very slightly longer than wide, the lobes 6–10 to (type of *Cephalozia badia*) 11–14 cells wide at base; lamina 16–22 or (type of *C. badia*) 28–32 cells wide. Cells quadrate to rectangular, thin to slightly firm-walled, 19–30 μm wide × 24–38 μm long; basal cells considerably larger; surface minutely papillose or smooth. Underleaves absent or, sporadically, rather large, lamellate, occasionally bifid. Gemmae lacking.

Dioecious (or autoecious?). Androecia on long shoots or rather short ventral-intercalary branches, occasionally on lateral-intercalary branches, the androecia becoming intercalary, wider than sterile sectors, with bracts more closely imbricate than leaves; antheridia 1 per bract. Gynoecia on long shoots or short ventral-intercalary branches; bracts in 2–3 series, larger than leaves, the innermost 2(3)-lobed to 0.35–0.45, the lobes acute to narrowly rounded, entire, but at times with 1–2 crescentic shoulders or rounded incipient lobes toward base, the lamina margins entire; the sinus base gibbous; bracteole similar to bracts. Perianth long-exserted, fusiform, obscurely trigonous, plicate above, moderately narrowed toward mouth, the mouth crenulate-denticulate to plurilobulate-dentate and then with teeth often curved, composed of a uniseriate row of 2–3 cells long or 2 cells wide at base and 2–3 cells long.

Capsule (Bednarek-Ochyra et al., 2000) ovoid-cylindrical, the wall bistratose; outer layer of cells subquadrate, with two-phase ontogeny ill-defined, the longitudinal walls with nodulose thickenings alternating with walls either lacking thickenings or with sinuous thickenings; inner wall with semiannular bands, the bands narrow.

Spores 11–14 μm in diam., papillose, the spore:elater diam. ratio 2:1. Elaters bispiral.

Distribution and Ecology: New Zealand: Campbell Island (380 m; see also Schuster, 2002a), South Island (1615 m). Also known from the South Sandwich Islands, South Orkney Islands, South Shetland Islands, west Antarctic Peninsula (see Bednarek-Ochyra et al., 2000), South Georgia, Falkland Islands (Engel, 1990a), Brunswick Peninsula (Engel, 1978) and western Patagonia (Hässel and Solari, 1985).

In New Zealand occurring with *Lophozia autoica*, *L. excisa* and *Pachyschistochila colensoana* at 1615 m over peaty soil along a small, permanently wet seepage area near the top of the "Old Man" (Old Man Ra., Otago, *Schuster 67-515c*, *67-516*, F).

Comments: Mature shoots have cupped, vertically oriented leaves, inserted to the stem midline dorsally, with the dorsal bases of the leaves lying over the stem. The leaves are uniformly bilobed, the lobe apices often blunt or only subacute and not drawn out, and the cells at the lobe tip are about as wide as long or at most slightly longer than wide. Branching is typically *Frullania* type, with ovate half-leaves distinct. Plants are whitish green to brownish to purplish brown.

The sexuality of the species remains uncertain. The type is apparently sterile, and Bednarek-Ochyra et al. (2000) studied only ♀ and sterile plants. Plants of *Schuster 67-515c* have both gynoecia and androecia. In most instances gametangia were observed on rather long branches, and a clear connection between ♂ and ♀ axes could no longer be established. In one case, however, a rather long perianth-bearing axis originated as a ventral-intercalary branch from an older shoot, and 1 or 2 gyres distant on the older shoot, a rather long androecial shoot originated as a ventral-intercalary branch. In another case, a long leafy shoot bore 2 rather long ventral-intercalary branches within 1 gyre of one another, one branch with a perianth, the other with an androecium. At some distance from these fertile branches the leafy shoot also bore 2 rather short ventral-intercalary branches in close proximity, both androecial. The plant is thus, at least in part autoecious, but this should be confirmed with study of other populations.

One of us (JJE) has studied leaves from the type of *Cephalozia badia* mounted on a slide (ex herb. Schuster). Lobes are 11–14 cells wide at the base, subacute to narrowly rounded at the summit and terminate in 2 laterally juxtaposed cells, a single cell, or exceptionally a uniseriate row of 2 cells; the cells at the tip are about as wide as long. The disc is 28–32 cells wide at the widest point, the disc cells are thin-walled, the median disc cells are 19–28 × 28–35 μm and the basal cells are considerably larger.

Cephalozia pachygyna R.M.Schust. *ex* J.J.Engel

Cephalozia pachygyna R.M.Schust., Beih. Nova Hedwigia 119: 25, 29. *f. 220, 221*. 2002, *nom. nud. Cephalozia pachygyna* R.M.Schust. *ex* J.J.Engel, Novon 17: 313. 2007. Holotype: New Zealand, South Is., Fiordland, *Schuster 84-138* (herb. Schuster).

Plants soft, loosely creeping, whitish green, no secondary pigments seen (plants observed only in non-exposed niches). Branches of *Frullania* type, the half-leaf ovate to sublanceolate; ventral-intercalary type branches common. Stems with cortical cells in 12–13 rows, firm-walled, not sharply differentiated, slightly to at most moderately larger than those of the medulla; medullary cells firm-walled. Rhizoids scattered, hyaline. Leaves vertically oriented, strongly dorsally assurgent, variably spreading, suberect to obliquely so, distant to contiguous, succubously to subtransversely oriented, the insertion weakly to strongly succubous, extending virtually to stem midline dorsally (the basal cell of leaf impinges on stem midline), the leaves concave, ovate (at times narrowly so), uniformly bilobed to 0.4–0.5; lobes incurved, at times abruptly so and the lobe tips then claw-like, moderately to narrowly acute, the apices terminating in a single cell or a uniseriate row of 2 cells at most slightly longer than wide, the lobes 8–10 cells wide at base; lamina 12–14 cells wide. Gemmae lacking. Underleaves absent.

Autoecious. Androecia on slender ventral-intercalary branches. Gynoecia on leading shoots; bracts much larger than leaves, narrowly elliptic-ovate to sublinear, 2-lobed. Perianth ca. 0.5 exserted, narrowly elliptic, terete below, trigonous distally, weakly plicate above, the mouth crenulate to crenate-feebly denticulate; perianth base 4–6-stratose.

Capsule ellipsoidal, the wall with outer layer of cells subquadrate to narrowly short-rectangular, with two-phase ontogeny ill-defined, the longitudinal walls with nodular to spur-like thickenings alternating with walls either lacking thickenings or with sinuous thickenings; inner wall with semiannular bands, the bands narrow, at times incomplete.

Spores and elaters not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1650 m).

Known only from a few collections. Occurring deep in a protected pocket of an outcrop at 1650 m in the alpine zone (area immediately below summit of Avalanche Peak, Scotts Track, Arthur's Pass Natl. Park). The type is from Fiordland.

Comments: The following combination of features are distinctive for the species. The leaf insertion extends to the stem midline dorsally, with leaf lobes 8–10 cells wide at the base and terminating in a single cell or a uniseriate row of 2 at most weakly elongated cells. Underleaves are completely lacking. Stem anatomy should be examined: Cortical cells are in 12–13 rows of firm-walled cells that are only slightly larger than medullary cells. The perianth base is fleshy, being 4–6-stratose, and the perianth mouth is crenulate, with only weakly elongated cells (at most 2:1). Plants develop brownish to purplish pigmentation in exposed sites, and asexual reproduction is lacking. The type is illustrated in Schuster (2002a, figs. 220, 221).

Cephalozia schusteriana J.J.Engel

Cephalozia schusteriana J.J.Engel, Novon 17: 313. 2007. Holotype: New Zealand, South Is., Canterbury Prov., Arthur's Pass Natl. Park, Scotts Track to Avalanche Peak, W of town of Arthur's Pass, 1370–1430 m, *Engel 22067 – c. per.* + ♂ (F); isotype: (CHR).

Plants soft, flexuous, lax, the main axis prostrate, pale whitish green on ventral and lateral sides of stem and at least the ventral half of leaves, the dorsal surface of stem and dorsal half of leaves magenta, the leading shoots to 700 μm wide. Branching copious, crowded, the branches weakly to strongly ascending, rather long, straggly and more heavily pigmented than main shoot (especially in distal sector of branch), notably more slender than the leading shoot, with a few branches (ventral-intercalary) soon becoming robust and of similar stature to leading axis, the branches mostly of ventral-intercalary type; *Frullania*-type branches less frequently, the half-leaf distinct, ovate; stoloniform branches occasional, of *Frullania* type, these unbranched. Stems with cortical cells in 11–13 rows, somewhat firm-walled, slightly to moderately larger than those of the medulla; medullary cells somewhat firm-walled. Rhizoids scattered, hyaline or brownish. Leaves (main shoot) dorsally assurgent, variably spreading, suberect to obliquely spreading, distant, strongly succubously inserted, the insertion extending virtually to stem midline dorsally, the leaves distinctly concave, broad ovate to ovate-subquadrate, uniformly bilobed to 0.4–0.5; lobes usually incurved, not drawn out, acute, at times somewhat apiculate, 5–8 cells wide at base, terminating in a single cell or a uniseriate row of 2 cells, the tip cell of lobes slightly longer than wide (to 2.4:1); lamina 20–24 cells wide. Cells markedly leptodermous, 22–34 μm wide × 44–54 μm long; surface smooth. Underleaves locally developed, lamelliform, short-bifid.

Autoecious. Androecia on rather short ventral-intercalary branches, becoming intercalary, with a few gyres of vegetative leaves prior to production of androecium; bracts loosely imbricate, leaf-like except for the slightly swollen basal sector and the slightly incurved tooth at dorsal base; antheridia 1 per bract. Gynoecia on ventral-intercalary branches with ca. 3–4 gyres of vegetative leaves, with a dense tuft of colorless rhizoids near base of lowermost bracteole; bracts in 3 series, those of innermost series sheathing base of perianth but the lobes stiffly reflexed-spreading, the bracts narrowly ovate-elliptic, bifid to ca. 0.45, the lobes narrowly acute, tapering to a single cell, the lobe margins weakly reflexed, entire, the lamina margins on each side with 1–2 blunt teeth; bracteole of lowermost series undivided and lamelliform, of second series much larger and bifid, the innermost bracteole ca. 0.75× bract area, narrowly connate on one side, free on the other, narrowly ovate-elliptic, short-bifid (to ca. 0.15), the lamina margins entire. Perianth rather long-exserted, subfusiform, trigonous throughout, plicate above, the mouth lobulate-ciliolate, the teeth of (1)2–4 elongated (3.1–4.1:1) cells, the tip cell tapering to the summit; perianth 1(2)-stratose toward base.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (1370–1430 m).

Known from only a few collections; occurring on the lip of a pool at 1370–1430 m in the alpine zone (type locality).

Comments: Perianths should be carefully searched for, since this is the only one of our *Cephalozia* species with a ciliolate perianth mouth. The teeth are numerous, each composed of (1)2–4 elongated cells (2–4.5:1) that are free laterally. The other three New Zealand species have a crenulate or at most crenulate-denticulate perianth mouth, and never have armature with a uniseriate row of 2 free cells. Also, the perianth base is 1–2-stratose and not fleshy as in *C. pachygyna*. Stems have 11–13 rows of somewhat firm-walled cortical cells that are only slightly to moderately larger than the medullary cells. The leaf insertion extends to the stem midline dorsally, and the lobes are 5–8 cells wide at the base and terminate in a single cell or a uniseriate row of 2 at most slightly elongated cells. Underleaves are locally developed on sterile shoots, and are undivided and lamelliform or short-bifid.

This species appears to be the same as "*Cephalozia ciliolata*," which is twice mentioned by Schuster (2002a), once in the key (p. 25) and again on p. 29. However, since there is no description, illustration or citation of a specimen of "*Cephalozia ciliolata*" in Schuster (2002a), that name therefore remains open to uncertainty.

Subg. ***Cephalozia***

Cephalozia austrigena R.M.Schust. *ex* J.J.Engel

Cephalozia bicuspidata subsp. *austrigena* R.M.Schust., Hepat. Anthocerotae N. Amer. 3: 712. 1974, *nom. inval. sin. descr. lat. Cephalozia austrigena* R.M.Schust., Beih. Nova Hedwigia 119: 29. *f. 222*. 2002, *nom. inval. typ. et herb. non. cit. Cephalozia austrigena* R.M.Schust. *ex* J.J.Engel, Novon 17: 312. 2007. Holotype: New Zealand, South Is., Mt. Aspiring Natl. Park, Mt. Brewster, NE of Haast River, ca. 4200 ft., *Schuster 67-451d* (herb. Schuster).

Plants whitish green, with sun forms developing intense vinaceous to carmine pigments, without trace of brownish pigments. Branching common, the branches frequently of *Frullania* type; ventral-intercalary type branches also present. Stems with cortical cells in 8–13 rows, inflated and forming a distinct hyaloderm, with cells much larger than the medullary cells, the ventral cortical cells smaller than the dorsal and lateral ones; medullary cells in 8–12 rows. Leaves dorsally assurgent, with insertion strongly succubous to subtransverse, not extending to stem midline dorsally, delimiting a leaf-free strip of 2 cells broad, the leaves concave, suborbicular-ovate, not decurrent dorsally, bilobed to 0.45–0.6; lobes rather sharp, usually connivent, lanceolate, terminating in 2–3 elongated cells, the tip cell to 2.7:1, at times rather sharply tapering to the summit, the lobes 4–5 cells wide at base; lamina to 10–17(20) cells broad. Cells in median sector 20–28 μm wide × 24–30 μm long to 24–31 μm wide × 36–65 μm long. Underleaves absent. Asexual reproduction nearly always present, by 1-celled, broad-elliptic gemmae.

Plants autoecious. Androecia on rather short ventral-intercalary branches; bracts leaf-like except more closely imbricate and with lobe cells less elongated. Gynoecia on axes of variable length, some on short ventral-intercalary branches; bracts in 2 progressively larger series, concave to canaliculate, ovate to elliptic, bifid to 0.4–0.5, the lobes narrowly acute, terminating in a single cell or a uniseriate row of 2 at most slightly elongated cells, the lobe margins entire, the lamina margins entire or with a broad-based small tooth; bracteoles very narrowly connate with bract on 1 side, free on the other, smaller than bracts, obovate, bifid to 0.35, the lobes rounded to subtruncate, the lobe and lamina margins entire. Perianth trigonous throughout, but more distinctly so above, gradually narrowed toward mouth; mouth crenulate-denticulate by cells laterally free for varying distances, some nearly entirely free laterally, the cells firm-walled, to 6:1, tapering to a narrowly rounded summit.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1280–1830 m), North Island (2025 m).

A species of the alpine zone, occurring, for example, admixed with *Pseudocephalozia lepidozioides* under dead tussock blades between edges of two tarns (E slope of Robert Ridge in vicinity of Mt. Robert Skifield, 1400–1480 m, Nelson Lakes Natl. Park). Above Sealy Lakes

(Sealy Ra., Mt. Cook Natl. Park) plants occurred at 1370–1495 m with *Pachyschistochila* sp., *P. trispiralis* and *Allisonia cockaynei* on damp soil over rocks in a late-snow area (*Schuster 48701A*, F). The type (Mt. Brewster) is cited as occurring with *Phyllothallia nivicola*, *Allisonia cockaynei*, *Balantiopsis diplophylla* and *Pseudocephalozia* cf. *lepidozioides*. Also on a soil layer between boulders in an area of cliffs and outcrops with scattered alpine plants at 2025 m (N slope of Mt. Ruapehu, S of Top of the Bruce, Tongariro Natl. Park, *leg. Engel*). The last is among a small suite of species known at the highest recorded elevation in New Zealand.

Comments: The species was once regarded as a subspecies of the widespread, basically Holarctic *Cephalozia bicuspidata*. It differs from that species in a) the intense vinaceous to carmine pigmentation, without trace of brownish coloration; b) the inflated, very large dorsal and lateral cortical cells, forming a distinct hyaloderm; and c) the often connivent leaf lobes. The description above is adapted and modified from Schuster (1974a, 2002a).

Family **CEPHALOZIELLACEAE** Douin

Cephaloziellaceae Douin, Bull. Soc. Bot. France 29: 1, 5, 13. 1920.

Plants typically strongly anisophyllous, exceptionally (*Amphicephalozia*) wiry, tending to be long and stringy, usually creeping (except *Allisoniella*), green but becoming brown, red-brown, fuscous or vinaceous in exposed sites, small to minute, to 350 μm wide, exceptionally to 500 μm wide. Branching often sparing and irregular, remote, the branches typically all or mostly of ventral-intercalary type; lateral-intercalary branches in some taxa; *Frullania*-type and/or *Acromastigum*-type branches present in a few species; stoloniform geotropic axes sometimes present. Stems usually wiry and firm, with cortical cells similar in size and form to medullary cells, or sometimes smaller, thick-walled and in 1–2 layers, a hyaloderm never present; medullary cell walls thin to firm. Rhizoids usually freely developed, never in dense fascicles, scattered (in *Allisoniella* mostly on flagelliform axes). Leaves usually small (except *Allisoniella*), usually transverse and vertically oriented (in ours), in some weakly to clearly succubous (incubous in *Cephalojonesia*), inserted dorsally to stem midline (except *Cylindrocolea* and *Cephaloziopsis*); leaves distant to contiguous, rarely imbricate, the stem usually extensively exposed, nearly always deeply bifid, unlobed (in some *Kymatocalyx* spp.) or retuse (*Cylindrocolea*), the lobes (when present) mostly narrowly acute, often divergent (when leaves flattened), the leaf margins entire or dentate. Cells usually very small, mostly only 7–15 μm wide in leaf middle, short-oblong and under 1.5:1, the walls thin to more often weakly to strongly, evenly thickened, without trigones; surface smooth or with low to coarse papillae. Oil-bodies small, usually 2–12 per cell, finely granular to subhomogeneous. Underleaves usually unlobed and range from small and lanceolate or ovate-lanceolate, to only 1–6-celled and vestigial, or reduced to ephemeral slime papillae visible only near shoot tips, exceptionally to 0.45 the area of leaves (often subequal to leaves in *Amphicephalozia*). Asexual reproduction by 2-celled gemmae produced in branched chains from uppermost leaf lobes on modified or unmodified leafy shoots.

Dioecious, autoecious or paroecious. Androecia nearly always on leafy axes or, at times, on abbreviated, leafless, ventral-intercalary branches, the androecia becoming intercalary, spicate, at times diffusely so; bracts bilobed like leaves (rarely obscurely so), pouched at base; antheridia nearly always 1 per bract, the stalk short, usually uniseriate. Gynoecia on leading leafy axes, occasionally on short ventral-intercalary branches lacking normal leaves; peri-

gynium completely absent; bracts larger than and clearly differentiated from leaves, bilobed, often toothed even when leaves are entire; bracteole somewhat smaller than to subequal or equal to bracts (in *Cephaloziopsis*) reduced or vestigial, usually connate with one or both bracts. Perianth emergent to long-exserted, deeply 3–5-plicate, weakly to at most moderately narrowed to the usually wide, truncate, crenulate to ciliolate mouth, the cells at mouth usually thick- or thin-walled and strongly elongated.

Seta with 4 large outer + 4 much smaller inner rows or, occasionally, 8 large outer + 4–14 much smaller internal cells. Capsule ellipsoidal, the wall bistratose, or (*Allisoniella*) 3–4-layered; outer layer of cells with one-phase development, usually with discrete nodular thickenings on almost all longitudinal and many transverse walls; innermost layer of cells similar in size and shape, with weaker nodular thickenings sometimes extended as tangential spurs but rarely extending across the tangential wall.

Spores finely papillose to verruculose, very small, 6–13 μm in diam., subequal to elaters in diam., rarely 1.5–2× as large. Elaters rather stiff, at most feebly tortuous, little tapered toward the ends, bispiral.

Type: *Cephaloziella* (Spruce) Schiffn.

The *Cephaloziellaceae* consist of eight genera, mostly very poorly understood. *Allisoniella* E.A.Hodgs. has five species, all south temperate. *Amphicephalozia* R.M.Schust. has two species, one, *A. amplexicaulis* R.M.Schust., from southern Chile, the other is *A. geisslerae* Pócs & Váňa from Madagascar (Pócs and Váňa, 2001). *Cephalojonesia* Grolle & Vanden Berghen is monotypic and occurs in Central Africa and Mexico (Burghardt et al., 2006). *Cephalomitrion* R.M.Schust. is monotypic and occurs in Australasia. *Cephaloziella* (Spruce) Schiffn. is world-wide. *Cephaloziopsis* (Spruce) Schiffn. has two species in the Neotropics and one in eastern Asia. *Cylindrocolea* R.M.Schust. has ca. 12 species, among them *C. atroviridis* (Sim.) Váňa of South Africa, *C. novae-caledoniae* (Grolle) R.M.Schust. of New Caledonia and *C. tagawae* (N.Kitag.) R.M.Schust., also of New Caledonia. *Kymatocalyx* Herzog (= *Stenorrhipis* Herzog) has four species and is pantropical. One, *K. africanus* Váňa & Wigginton, occurs in Africa (Tanzania [1600–2350 m] and Malawi [1200–2220 m]), one on the East African Islands (Madagascar, Mauritius, Réunion and Comoro Archipelago), one Neotropical and the last occurs in Malaysia, Sarawak, Sumatra and several stations in the Neotropics (see also comments in Schuster, 2002a).

Except for *Allisoniella* the species are so small that manipulation and study of material are very difficult and casual identification of material is almost prohibitively difficult. Vegetative differences often are not wholly reliable to distinguish between the genera, and, for generic determination, mature sporophytes should be carefully searched for, notably for seta cross sections. For species determination it is necessary to carefully dissect out whole plants in order to determine the sexuality.

The family includes three genera that are relatively primitive in having a more massive seta of the 8+4 or 8+4–12 type. These are *Allisoniella* and *Cephalomitrion* of our area and *Amphicephalozia*. The remaining genera all have a reduced, 4+4-type seta, which is very unusual in hepatics. For example, this seta type is also found in the unrelated Neotropical family *Phycolepidoziaceae* R.M.Schust. of the *Lepidoziineae*.

Cephalomitrion R.M.Schust.

Cephalomitrion R.M.Schust., Nova Hedwigia 61: 350. 1995.

Plants rigid, maximally wire-like, thread-like, pitch-black, the shoot tips and gynoecial regions often deep magenta, at times the stems pure green and the leaves claret-red, the plants small, 160–245 μm wide with leaves, but broader in ♂ and ♀ sectors, with shoots densely interwoven and, especially toward the base of the plant, entrapped with fine grains of sand. Branching common, irregular, the shoots often elongating and becoming arcuate, the branches all ventral-intercalary, at right angles to parent axis, apparently originating from near ventral angle of lateral leaves; geotropic stolons lacking. Stem filiform, the cortical cells in 1–2 layers, deep brown to blackish, rather firm-walled, larger than medullary cells; medullary cells very thick-walled, scarcely pigmented, the lumina rounded to guttulate. Rhizoids few or none, scattered and usually solitary. Leaves unistratose, so closely appressed to stem as to be almost invisible, remote below, contiguous to feebly imbricate toward shoot apices, scale-like, strongly concave, swollen just above insertion and forming a transverse ridge, the insertion transverse, extending to stem midline dorsally; leaves (when flattened) rounded-quadrate to suboblate-quadrate, (160)180–200(230) μm wide and long, larger in and near gynoecial sectors, bilobed to (0.25)0.35–0.5; lobes subacute to most often blunt at the tips, mostly 8–12 cells wide at base, the margins and sinus never reflexed, the margins vaguely crenulate by tumid cells, otherwise entire, the marginal cells not differentiated; sinus V-shaped, acute. Cells firm-walled above, thin in basal sector, lacking trigones, characteristically tumid, gibbous near margins (best seen in partial profile), irregular in shape and size, the median cells 9–11(13) × 12–15(18) μm, the lobe marginal and intramarginal cells 8–11(13) × 11–15 μm, the basal scarcely larger; surface smooth. Oil-bodies occupying a conspicuous portion of the cell, pale smokey grey, 4–8 per median disc cell, obscurely and indistinctly granular, with a hazy appearance, 3–4 μm and spherical to (2.8)3–3.5 × 5–6.5 μm, sporadically 5 × 6 μm. Chloroplasts large for cell size. Underleaves reduced to a spherical, papilliform cell, but near gynoecia sometimes narrow, comprised of 4–5 cells. Asexual reproduction absent.

Dioecious (the ♂ and ♀ plants usually intermingled), or, at least sometimes, autoecious. Androecia becoming intercalary, the bracts in 2–3(4) pairs, abruptly larger than adjacent sterile sectors, leaf-like but pouched in dorsal half of bract base; antheridia 1 per bract, the stalk uniseriate. Gynoecia terminating axes of various lengths, somewhat clavate-capitate, usually claret-red, not innovating; bracts polymorphic, in 2–3 series, those of innermost series closely sheathing perianth, concave, bilobed, the lobes triangular, the apices blunt to rounded, the lobe margins crenulate by tumid cells, otherwise entire; bracteole conspicuously connate with bracts on both sides, ovate, unlobed. Perianth ca. 0.45–0.55 emergent, slightly narrowed to the wide mouth, deeply 4(5)-plicate, the mouth often decolorate with age, obscurely crenulate with variable, only sporadically elongated cells; perianth 2-stratose at base, becoming unistratose below the middle.

Seta with 8 outer rows of cells and 4 rows of much smaller internal cells. Capsule ovoid to short-ellipsoidal, the walls 2-stratose; outer layer of cells variable but mostly rectangular, with one-phase ontogeny, the longitudinal walls all, with rare exceptions, and some or many transverse walls with well-defined nodular thickenings; inner layer of cells less regular, with delicate nodular thickenings on longer walls, often with weak semiannular bands.

Spores purplish brown to reddish brown, 9–10 μm in diam., almost smooth. Elaters weakly sinuous, 6–8 μm in diam., bispiral, the spirals rather broad, 2–2.2 μm wide.

Type: *Cephalomitrion aterrimum* (Steph.) R.M.Schust. (≡ *Cephalozia aterrima* Steph.)

A monotypic genus of Australasia. Description freely modified from Schuster (1995a).

References: Schuster (1972a, 1995a, 1996a, 2002a).

Cephalomitrion aterrimum (Steph.) R.M.Schust.

[Fig. 128: 3, oil-bodies, p. 558]

Cephalozia aterrima Steph., Sp. Hepat. 3: 331. 1908. *Cephaloziella aterrima* (Steph.) E.A.Hodgs., J. Roy. Soc. New Zealand 2: 109. Mar. 1972; (Steph.) R.M.Schust., Nova Hedwigia 22: 212. 31 Dec. 1972 (1971). *Herzogobryum aterrimum* (Steph.) Grolle, J. Bryol. 11: 326. 1980. *Cephalomitrion aterrimum* (Steph.) R.M.Schust., Nova Hedwigia 61: 554. 1995. Type: Tasmania, Mt. Wellington, *Weymouth*.

Herzogobryum filarium Grolle, Feddes Repert. 86: 73. 1975. Type: Tasmania, Lake St. Clair, on lake shore, *Scott 574*.

The generic description serves to characterize the species.

Distribution and Ecology: New Zealand: Stewart Island (5 m), South Island ([180]850–1590 m), North Island (1450–1700 m); Australia: Tasmania, Victoria, New South Wales.

In New Zealand known from Fiordland, Otago, Westland, Canterbury, Western Nelson and Volcanic Plateau (Mt. Ruapehu) EPs. In South and North islands a plant of the penalpine and alpine zones, particularly alpine fellfields. Plants typically form compact, flattish to dome-like, thin to rather thick, at times extensive blackish mats over exposed rock or silt of streambeds. Plants typically occur on exposed flat bedrock or over downward, flattish and angling bedrock of creek beds or over small rocks, but in all of these cases *Cephalomitrion* is found where a thin to thick layer of soil has accumulated (at times ca. 3 cm thick) and where water flow is constant, even if only at a trickle level. The mats lightly adhere to the streambed substrate, or, more often, are firmly anchored to the rock substrate, with slow-moving water flowing over them. Plants are likely to be saturated for all or most of the period that they are not under snow cover. On Stewart Island *Cephalomitrion* was found at the base of Belltopper Falls (Port Pegasus, immediately below North Arm) at only ca. 5 m in an open, humid niche dominated by bedrock with a forest margin of *Weinmannia racemosa* and *Dracophyllum*. In the upper Otira valley (Arthur's Pass, 870–960 m) on surfaces of greywacke boulders in small stream channels, in penalpine *Dracophyllum rosmarinifolium – Chionochloa conspicua* shrubland. At Mt. Euclid (Paparoa Ra., Westland, 1280 m) it was on granite stones set in a tarn, surrounded by *Chionochloa australis* grassland. On the Young Ra. (SE of Haast Pass, Otago, 1150 m) it was on rocks at the side of a cascading snow-melt stream in *Schoenus pauciflorus – Chionochloa crassiuscula* tussockland. It is most notably found with *Isophyllaria attenuata*; the two share very similar habitat preferences. Other accompanying species are *Allisoniella nigra*, *Andreaea acuminata*, *Diplophyllum verrucosum*, *Ditrichum strictum*, *Hepatostolonophora rotata*, *Isotachis montana*, *Kurzia helophila*, *Marsupella sparsifolia* subsp. *childii*, *Rhacocarpus purpurascens* and *Siphula decumbens*.

Mats are comprised of densely interwoven shoots, and the basal part of the mat often consists of root-like masses of old, dead plant bases that form a mesh that entraps grains of sand and very fine gravel. This appears to provide a notable firmness to the mat that is conducive to withstanding a flow of water after heavy rain or strong snow melt.

Comments: Plants have the size, aspect, color, and small, scale-like, bifid leaves of a *Cephaloziella*, but differ from that genus in the seta, with 8 rows of outer cells and 4 rows of much smaller internal cells; *Cephaloziella* has a seta of the 4+4 type. Several vegetative differences between the genera are useful. Plants of *Cephalomitrion* appear leafless due to the erect and markedly appressed leaves vs. moderately to widely spreading and distinct in *Cephaloziella*. *Cephalomitrion* also differs in stem anatomy, with a somewhat differentiated cortex of 1(2) strata of relatively thin-walled cells, distinct from the many rows of smaller, notably thick-walled, medullary cells each with a small lumina. *Cephaloziella* has stems with a cortex of firm-walled cells and medullary cells thinner-walled. *Cephalomitrion* lacks gemmae whereas they are typically present in *Cephaloziella*. Also, the leaf cells in *Cephalomitrion* tend to be clearly gibbous, especially near the margins.

Schuster (1996a, p. 14, 47) used the name *Cephalomitrion aterrimum* var. *longiscyphum*, *nom. nud*. for a plant from Tongariro Natl. Park. We have not seen the specimen.

Allisoniella E.A.Hodgs.

Allisoniella E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 80. 1965.
Protomarsupella R.M.Schust., J. Hattori Bot. Lab. 26: 216, 279. 1963, *nom. inval.*, *sin. descr. lat.*; Rev. Bryol. Lichénol. 34: 264. 1966. Type: *P. scottii* R.M.Schust.

Plants rigid, the leafy shoots stiffly ascending to erect, arising from a system of creeping or geotropic, stoloniform axes, the shoots small-leaved below, larger-leaved and denser above, vinaceous to deeply fuscous or piceous (the older sectors often bleached), the shoots relatively vigorous, 410–925 μm wide. Branching copious, the erect leafy shoots not or scarcely branched above, the branches arising from a system of plagiotropic or geotropic, densely rhizoidous, whitish stoloniform branches, the leafy branches occasionally arising from small-leaved basal sectors of erect shoots which originate from plagiotropic axes by suddenly becoming phototropic, the branches usually all ventral-intercalary. Stems with cortex well differentiated, in (1)2–3(4) layers of thick-walled, pigmented cells; medullary cells somewhat to considerably larger, hyaline, thin-walled. Rhizoids on stoloniform axes, lacking on erect leafy shoots. Leaves pectinate-distichous, rather stiffly and widely spreading to subsquarrose, at times rather dense above, transversely oriented, the insertion extending to stem midline dorsally, the leaves often weakly folded or conduplicate, usually bifid to 0.5–0.9; lobes often shallowly adaxially convex or abaxially sulcate at least near gynoecia, with margins (and often sinus) decurved; lobes 15–28 or more cells broad, mostly sharp, the margins entire or feebly crenulate because of projecting cell walls. Cells thick-walled, without trigones, small, the median cells 9–14 × 10–18 μm; surface usually papillose, at times strongly so. Oil-bodies (Schuster, 2002a) 2–4 per cell, rather large, finely granular or finely papillose. Underleaves completely lacking in vegetative sectors. Gemmae rarely developed, colorless or vinaceous, smooth, ellipsoidal, 8.5–10.5 × 14–17 μm.

Autoecious (except probably *Allisoniella nigra*). Androecia on long leafy shoots, mostly becoming intercalary, compactly spicate; bracts leaf-like but denser, the base concave; antheridia usually single per bract, the stalk 6 cells long, uniseriate. Gynoecia on leading shoots or elongated, often leading, ventral-intercalary branches, the innermost bracts in 2–3 gradually larger series, deeply bifid, like leaves but larger and with margins crenulate-denticulate to denticulate, the lobes usually clearly abaxially sulcate, blunt to sharp; bracteole unlobed or bilobed, connate on both sides with bracts by at least 0.25 to form a distinct sheath around perianth

base. Perianth often purplish, long-exserted, deeply and longly 4–5-plicate, the plicae compressed and rib-like and extending nearly to perianth base, the mouth bleached, shallowly and irregularly lobulate, crenulate to feebly denticulate by cells that are weakly to moderately elongated, thick-walled and varying from free only at the tips to completely free.

Seta with 8 rows of outer cells and (3)4–14 rows of internal cells. Capsule ellipsoidal, the wall 2(?) to 3–4-stratose; outer and innermost layers both with small, sharply defined, well-spaced, nodular thickenings, those of the inner layer rarely with short tangential extensions.

Spores 7–11.5 μm in diam., weakly verrucose-papillose or nearly smooth. Elaters 7–9 μm in diam., bispiral.

Type: *Allisoniella nigra* subsp. *novaezelandiae* R.M.Schust. (= *Allisoniella obcordata* E.A.Hodgs.)

A genus of five species, four Australasian and one, *Allisoniella subbipartita* (C.Massal.) R.M.Schust. & J.J.Engel, from southern South America. Of the Australasian species, three occur in our area and one, *A. tasmanica* R.M.Schust., is endemic to Tasmania. The genus was described by Hodgson (1965) but was placed into synonymy under *Cephaloziella* by Grolle (1966d); Schuster (1972a) resurrected the genus and distinguished it from *Cephaloziella* on the basis of several criteria: a) *Allisoniella* has a seta with 8 rows of outer cells and 4–12 internal cells vs. a seta of the 4+4 type in *Cephaloziella*; b) the stem in *Allisoniella* is more rigid, with a well-defined 2–3-stratose cortex, vs. a defined cortex is lacking in *Cephaloziella*; c) plant architecture differs: *Allisoniella* normally has leafy axes arising from a system of ramified, microphyllous, plagiotropic or geotropic axes to which rhizoids are almost wholly confined, whereas *Cephaloziella* exhibits no such shoot dimorphism, and bears scattered rhizoids on normal leafy axes; and d) the capsule wall is 3–4-layered in *Allisoniella* vs. uniformly 2-stratose in *Cephaloziella*.

The stiffly ascending leafy axes in *Allisoniella* tend to be small-leaved below, larger-leaved above, and have an aspect close to that of *Marsupella sparsifolia*, also found in New Zealand. In the absence of fertile structures, *M. sparsifolia* differs from *Allisoniella* by the presence of lateral-intercalary branching and leaf cells with conspicuous trigones.

Description considerably modified from Schuster (1972a).

References: Schuster (1972a, 1996a, 2002a).

Key to Species

1a. Leaves (when flattened) usually wider than long, or, less often, as wide as long, the leaves (at least toward gynoecia) with sinus bases and lobes deflexed; lobe apex rounded or, if sharp, then the lobes abaxially sulcate, their apices never incurved; stem cortex 1–2(3)-stratose; perianth deeply 5-plicate; seta with 9–12(14) rows of interior cells; capsule wall 3–4-stratose. Sect. *Allisoniella* 2

2a. Leaves deeply bilobed to (0.55)0.7–0.9, folded, with a distinct, recurved keel, the sinus bases strongly gibbous; surface closely, coarsely papillose; stem cortex 1-stratose. Plants translucent green or pale brown . . . . . *A. recurva* (p. 576)

2b. Leaves shallowly bilobed to 0.1–0.55, not folded, the keel region not concave, not recurved at apex, the sinus bases not or weakly recurved; surface smooth to delicately papillose; stem cortex 2–3-stratose. Plants opaque, purplish to deep brown . . . . . *A. nigra* (p. 574)

1b. Leaves of sterile shoots (when flattened) oblong, longer than wide, with margins and sinus bases never recurved or deflexed; lobe apex acute, the lobes flat (adaxially concave only near gynoecia), their apices often gently incurved and oriented toward shoot apex; stem cortex (2)3–4-stratose; perianth normally deeply 4-plicate (cruciate in cross section); seta with only (3)4 rows of interior cells; capsule wall 2-stratose. Plants deep brown or fuscous or carmine; leaf surface with coarse papillae (7–8 × 10–12 μm). Sect. *Protomarsupella* . . . . . *A. scottii* (p. 572)

Sect. ***Protomarsupella*** (R.M.Schust.) R.M.Schust.

Protomarsupella R.M.Schust., Rev. Bryol. Lichénol. 34. 264. 1966. *Allisoniella* sect. *Protomarsupella* (R.M.Schust.) R.M.Schust., Nova Hedwigia 22: 150. 1972 (1971). Type: *Allisoniella scottii* (R.M.Schust.) R.M.Schust.

Allisoniella scottii (R.M.Schust.) R.M.Schust.

[Plate 12G]

Protomarsupella scottii R.M.Schust., Rev. Bryol. Lichénol. 34: 267. 1966. *Allisoniella scottii* (R.M.Schust.) R.M.Schust., Nova Hedwigia 22: 151. 1972 (1971). Holotype: New Zealand, Stewart Is., Tin Ra., 1200 ft., Jan. 1962, *Schuster 53107* (herb. Schuster).

Plants erect, carmine to blackish brown, at times appearing scorched, distinctly nitid when dry, the shoots (450)520–780 μm wide, with straight apices. Branching copious, irregular, with a system of abundant, often interwoven, creeping, microphyllous axes and erect, phototropic, leafy shoots, the erect leafy shoots toward their origin freely developing intercalary branches, microphyllous at least initially, often remaining stoloniform and either plagiotropic or geotropic, but mostly becoming erect and normal-leaved, the stolons often abundant; branches all ventral-intercalary. Stems firm, brown to deep brown, the cortex in (2)3–4 layers of thick-walled cells, the outermost layer in cross section with guttulate, elliptical lumina; medullary cells considerably larger, thin-walled. Rhizoids on leafy shoots rare or lacking. Leaves gradually larger upward, stiffly and widely spreading, pectinately distichous, never dorsally assurgent, contiguous, somewhat adaxially concave, but not canaliculate or folded, transversely oriented and inserted, not reflexed on sterile shoots, short-oblong to oblong-subquadrate to oblong-ovate, longer than wide, 375–400 × 310–340 μm to 470–510 × 340–400 μm, bifid to 0.4–0.5; lobes curved toward shoot apex or incurved, on flattened leaves only weakly divergent so that leaves are parallel-sided for most of their length, the lobes typically plane or slightly adaxially concave (rather than abaxially sulcate) but sporadically feebly and imperceptibly abaxially sulcate, acute, 14 or more cells wide at base, the tips plane or incurved, acute to blunt; sinus acute. Cells in vertical columns, thick-walled, the middle lamella at times darker, the cells very small, median lamina cells 8–12 μm wide × 12–16 μm long; marginal cells of lobes 8–11 μm wide; basal cells not distinctly elongated, 11–13 μm wide × (13)15–22 μm long; surface coarsely papillose with close to contiguous papillae or finely and inconspicuously papillose. Oil-bodies (Schuster, 1966a) (1)2–3(4) per cell, rather large, faintly granular, almost smooth, ellipsoidal or oblong-ellipsoidal to subspherical, (2.6)3–3.5 μm to 2.8–3.2(4) × 4.5–6(7) μm; marginal cells with smaller oil-bodies. Gemmae unknown.

Autoecious. Androecial branches often arising from the ♀ ones, or sometimes vice versa, the androecia eventually becoming intercalary, compactly spicate; bracts in 4–5(6) pairs, closely imbricate, the larger bracts ventricose at the base, with lobes often lower and blunter than on leaves; antheridia 1–2 per bract, the stalk uniseriate. Gynoecia terminal on long leafy axes, the bracts typically smaller than uppermost leaves, closely sheathing basal sector of perianth, ovate-quadrate, asymmetrically bilobed to 0.35, the dorsal lobe narrower and shorter, the lobe margins entire; bracteole large, connate for ca. 0.5 with bract on one side, but free or short-connate on the other side, oblong-ovate, bilobed to 0.35. Perianth long-emergent, without subtending perigynium, the mouth decolorate with age, oblong-ovoid or narrowly ovoid, deeply 4–5-plicate for 0.75 its length (and cruciate in cross section), rarely with lower accessory plicae distally, the perianth somewhat narrowed toward the mouth; mouth truncate, sinuous or entire to remotely crenulate with weakly projecting cells, the cells at mouth guttulate, with rounded lumina, similar to cells below them.

Seta with 8 rows of outer cells and (3)4 rows of internal cells. Mature capsules observed.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (360 m), South Island (1160–1310 m).

Allisoniella scottii forms fuscous to blackish patches over rocks or stones, at the edges of insolated shallow streams (Stewart Island) or with *Herzogobryum atrocapillum* and *Isophyllaria attenuata* on the edge of a small alpine tarn at 1160–1310 m in the Paparoa Ra. (NE of Mt. Euclid, headwaters of Awakiri River, South Island, *leg. Schuster*). Schuster (1996a, p. 13) remarked that the Paparoa Ra. plants "occurred in full sun, forming scorched patches, at the edge of a small alpine tarn, at the edge of the water line, forming a black crust—under conditions where submersion and desiccation regularly succeed each other." A specimen from the same locality (*Glenny 8117*) was found in a cushion bog on thin soil over stones, among *Oreobolus pectinatus – Donatia novae-zelandiae* cushionfield, with *Isophyllaria attenuata* and *Cephalomitrion aterrimum*.

Comments: This species has, when sterile, "an unmistakeable similarity to the scorched-appearing Marsupellae, such as *M. sparsifolia*" (Schuster, 1966a, p. 267), and, calling attention to this character, the species was initially placed in a genus *Protomarsupella* (Schuster, 1966a). Characters that suggest *Marsupella* are the geotropic, stoloniform axes issuing from the lower ends of leafy erect shoots; the stiffly spreading, deeply bifid leaves; the very narrow ventral merophytes, without a trace of underleaves; and the relatively large oil-bodies (for the cell size), mostly 2 or 3 per cell. However, the long, markedly emergent perianths and lack of a perigynium preclude any closer affinity to *Marsupella*. If only sterile plants are present, then branch type should be checked: branches are ventral-intercalary in *Allisoniella scottii* rather than lateral-intercalary in *Marsupella*.

Plants occur in small, pure mats, with a characteristic growth pattern: a dense mass of extensive plagiotropic and geotropic, leafless, interwoven axes gives rise to numerous erect leafy stems of limited height. The erect leafy shoots are of similar height. This is due to androecial shoots being determinate after forming at most 3 androecia, and gynoecia failing to innovate (see Schuster, 1996a for comments and also for remarks on sexuality).

Schuster (1996a, p. 10) remarked "erect leafy shoots that fail to produce gametangia are rare; indeed, shoots that remain sterile indefinitely probably do not exist." We have observed populations with many sterile shoots, with only a few perianths and androecia. As with some other *Cephaloziellaceae*, perianths mature even if fertilization fails to take place.

Sect. ***Allisoniella***

Allisoniella nigra (Rodway) R.M.Schust.

Sphenolobus nigrus Rodway, Tasman. Bryoph. 2: 33. 1916 (Pap. & Proc. Roy. Soc. Tasmania 1916: 83. 1917). *Cephaloziella nigra* (Rodway) Grolle, J. Jap. Bot. 41: 225. 1966. *Allisoniella nigra* (Rodway) R.M.Schust., Nova Hedwigia 22: 141. 1972 (1971). Type: Tasmania, Cradle Mtn.

Comments: This species has two subspecies, subsp. *nigra* of Tasmania and New Zealand, and subsp. *novaezelandiae* of our area. Grolle (1966d) and Schuster (1972a, fig. 3: 2–5) illustrated the type. Grolle (1966d) also placed *Allisoniella obcordata* E.A.Hodgs. into the synonymy of *A. nigra*. Schuster (1972a) described *A. nigra* subsp. *novaezelandiae*, and *A. obcordata* appears to be identical to that taxon. Schuster (1972a) provided formal recognition to a form, fo. *subobtusa* R.M.Schust., which has, when compared to fo. *novaezelandiae*, more deeply descending sinuses and leaf lobes more rounded.

There remains a question of sexuality of this species. *Allisoniella obcordata* was stated to be dioecious by Hodgson (1965); we have been unable to corroborate the Hodgson statement. Subspecies *novaezelandiae* is autoecious (Schuster, 1972a). In view of all these ambiguities, and because of the paucity of adequate material available, we continue to treat these three extremes as one species, as follows.

Key to the subspecific taxa

1a. Leaf lobes blunt to (more usually) narrowly to broadly rounded at the apex, to 32 cells wide at base. Autoecious. New Zealand. subsp. *novaezelandiae* 2
  2a. Leaves divided to 0.1–0.35; lobes broadly rounded . . . . . .fo. *novaezelandiae* (p. 575)
  2b. Leaves divided to 0.45–0.55(0.6); lobes usually blunt to only narrowly rounded . . . . . .fo. *subobtusa* (p. 575)
1b. Leaf lobes acute to (usually) subacute or blunt, but not rounded, to 24 cells wide at base. Dioecious (*fide* Hodgson, 1965) or autoecious. New Zealand [+ Tasmania]. subsp. *nigra* 3
  3a. Plants autoecious. New Zealand . . . . . var. *acutiloba* (p. 576)
  3b. Plants dioecious. [Tasmania] . . . . . var. *nigra*

Allisoniella nigra subsp. ***novaezelandiae*** R.M.Schust.

Allisoniella nigra subsp. *novaezelandiae* R.M.Schust., Nova Hedwigia 22: 143. 1972 (1971). Holotype: New Zealand, North Is., Waipoua River, N of Dargaville, *Schuster 63-1891* (herb. Schuster).
Allisoniella obcordata E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 80. 1965. Holotype: New Zealand, North Is., Waipoua River, *Allison H919* (MPN, Hodgson hb. No. 6165, *non vidi*).

Plants rigid, suberect to erect, with wiry stems, brownish to fuscous where not decolorate, the leafy stems 800–950 μm wide. Leaves strongly and stiffly spreading, remote to contiguous, unistratose except sometimes in one tier at stem juncture, nearly flat on weaker (and especially ♂) shoots, on vigorous stems the leaves with lobes distinctly abaxially concave (with

decurved margins) or (in extreme cases) sulcate, the leaves broadly orbicular-quadrate, always wider than long, (300)380–450 × (425)525–580 μm to 440–540 × 580–700 μm, in vegetative sectors with sinus varying from very slight, the leaves merely broadly retuse to bilobed to 0.1–0.55; lobes very wide (as wide as to much wider than long), 20–32 cells wide, the summit narrowly to more often broadly rounded and becoming semicircular; sinus occasionally gibbous; lamina margins broadly rounded at the base, sometimes cordate. Cells with walls thickened but not strongly so (the lumina remaining angular), the marginal cells subquadrate, usually 10–13 μm wide, the median cells 15–17 μm wide × 17–20(24) μm long; surface smooth or nearly so. Gemmae unknown (except in fo. *subobtusa*).

Autoecious. Androecia eventually intercalary on long leafy axes that often have reduced sterile leaves, compactly spicate, with 5–7 pairs of bracts; bracts closely imbricate, pouched, shallowly bilobed (sinus descending to 0.1–0.15), lobes broadly rounded, appressed to bract lying anterior. Gynoecia terminating long leafy axes, with leaves gradually larger and grading into bracts; innermost bracts broadly orbicular, almost reniform, wavy, bilobed to 0.25, the lobes broadly but shallowly abaxially concave, broadly rounded, semicircular. Perianth to 0.75 emergent at maturity, oblong in outline, at most feebly contracted to the truncate mouth, deeply (4)5-plicate in distal 0.6–0.75, the plicae compressed (perianth cross sections, above, cruciate or stellate), the mouth becoming bleached and decolorate, crenulate or crenulate-denticulate.

Sporophyte unknown.

Comments: This taxon, whatever its rank, is "clearly autoecious" (Schuster, 1972a, p. 144); the very similar *Allisoniella obcordata* is described by Hodgson (1965) as dioecious and with perianths 5-plicate. Schuster (1972a) examined a fragment of the type of *A. obcordata* and remarked (p. 144) "in the fragments I have seen androecial and gynoecial branches are obviously intermingled and I suspect the plant may prove to be autoecious, rather than dioecious as Hodgson describes.... No connection could be demonstrated between the long sexual branches, however." If the inflorescence differences actually exist, two taxa may be at hand.

Two forms have been recognized in the literature.

Allisoniella nigra subsp. ***novaezelandiae*** fo. ***novaezelandiae***

Leaves divided to 0.1–0.35; lobes broadly rounded.

Distribution and Ecology: New Zealand: North Island. Known only from the type collection, the Waipoua River (North Auckland).

Allisoniella nigra subsp. ***novaezelandiae*** fo. ***subobtusa*** R.M.Schust.

Allisoniella nigra fo. *subobtusa* R.M.Schust., Nova Hedwigia 22: 143. *pl. 5: 1–11*. 1972 (1971).
Holotype: New Zealand, Stewart Is., Pegasus Creek, *Schuster 49581a* (herb. Schuster).

Leaves at least locally 2-stratose toward their bases, broadly quadrate when flattened, a little broader than long (490–520 μm wide × 390–440 μm long), bilobed to 0.4–0.55, sporadically to 0.6; lobes to 27–32 cells broad at base, variable, tending to be concave and/or sulcate abaxially, as long or a little longer than broad, usually blunt to narrowly rounded (sporadically

acute to subacute); sinus obtuse to, infrequently, rectangular, often gibbous. Cells weakly thick-walled to almost guttulate with rounded lumina. Otherwise unknown.

Distribution and Ecology: New Zealand: Stewart Island. Known only from the type, which grew in a shallow stream over boulders subject to inundation.

Comments: Plants are intermediate between subsp. *nigra* and typical subsp. *novae-zelandiae*. It is similar to or approaches fo. *novaezelandiae* in the mostly broadly obtuse to narrowly rounded leaf lobes, but the leaves are bilobed as deeply as in subsp. *nigra*.

Allisoniella nigra subsp. ***nigra*** var. ***acutiloba*** J.J.Engel

[Fig. 128: 2, oil-bodies, p. 558]

Allisoniella nigra subsp. *nigra* var. *acutiloba* J.J.Engel, Novon 17: 313. 2007. Holotype: New Zealand, Stewart Is., Bald Cone, 80 m, *Glenny 9317* (F); isotypes: (AK, CHR 574634, HO).

Plants stiff and rigid, dark yellowish brown (but pale toward the shoot apices) to fuscous. Leaves widely spreading to squarrose, the lobes decurved gently, giving the overall aspect of a slightly adaxially convex leaf, the leaves bifid to 0.35–0.5; lobes 17–24 cells wide at the base, with margins slightly recurved, the lobes plane or weakly and inconspicuously abaxially sulcate, subacute to acute, terminating in a single cell or a uniseriate row of 2 ± isodiametric cells. Cells of the lamina and lower sectors of the lobes arranged in vertical rows; surface delicately and inconspicuously striate-papillose. Oil-bodies occupying moderate portion of cell volume, hyaline, 2–3 per median lamina cell, globose to broadly elliptic, finely papillose, the spherules slightly protruding beyond membrane. Chloroplasts large for cell and oil-body size.

Plants autoecious.

Distribution and Ecology: New Zealand: Stewart Island (30–80 m).

Occurring at ca. 30 m on bedrock submerged in water above Belltopper Falls (Port Pegasus, Stewart Island). On Bald Cone (Pegasus Harbor, Stewart Island, 80 m) it was found on granite bedrock in a small streambed, partially inundated, the streambed surrounded by *Leptospermum scoparium – Empodisma minus* scrub 50 cm high. Accompanying species were *Rhacocarpus purpurascens*, *Blindia robusta*, *Cheilolejeunea albovirens* and *Riccardia* sp.

Comments: With the addition of var. *acutiloba*, the subsp. *nigra* is added to the New Zealand flora. The variety appears to match the type of *Allisoniella nigra* of Tasmania except for sexuality. Clearly further study on the complex is necessary, particularly to establish presence of the dioecious condition for some populations of *A. nigra*.

Allisoniella recurva R.M.Schust.

Allisoniella recurva R.M.Schust., Nova Hedwigia 22: 146. *pl. 4: 7–11*; *5: 12–13*. 1972 (1971). Holotype: New Zealand, North Is., Mt. Egmont, *Schuster 48917a* (herb. Schuster).

Plants rigid, light, translucent green to olive-green (but stems becoming pale brown with age) to pale brown throughout, the shoots 450–600 μm wide, to 2.2 mm high, at times contorted, not straight. Stems with cortex in a single layer of very thick-walled cells; medullary

cells much larger, thin-walled. Leaves rigid, vertically oriented, stiffly and at times widely spreading to squarrose, contiguous to rather densely imbricate, the insertion transverse, the leaves 170–195 × 190–220 μm to 300–360 × 440–520 μm, bifid to (0.55)0.7–0.9, loosely conduplicate; lobes strikingly similar, markedly abaxially, broadly sulcate, erect but not incurved or if leaves squarrose then with lobes moderately incurved and weakly claw-like, variable in number of cells wide at base: (6)8–12 up to 19–28, the apex on sterile shoots acute and sharply pointed to subacute (and then terminating in a single cell or a uniseriate row of 2 cells) grading to narrowly rounded; sinus and margins strongly recurved, a distinct but abbreviated (0.2–0.3× leaf length) keel apparent that is often strongly arcuate or even semicircular. Cells subhyaline, with notably thickened, colorless walls, the marginal cells of lobes 10–11 μm wide × 12–17 μm long, the median lamina cells 12–16 μm wide × 14–19 μm long, hardly larger toward base; surface distinctly papillose, the papillae close and dense, notably evident in profile on leaf margins. Gemmae absent.

Plants autoecious. ♂ and ♀ Branches erect, from a common translucent brown, plagiotropic axis; ♂ branches ending in a spicate, tapered androecium (often with an intercalary branch from its base that is soon gynoecial); ♀ branches remaining simple, ending in a gynoecium, which often innovates, the innovation soon androecial. Perianths 4–5-plicate, the shallowly lobulate mouth fringed by strongly elongated (4–5:1) thick-walled cells, whose distal 0.2–0.35 are free to form finger-like extensions that are 7–10 μm wide basally × 30–38(40) μm long.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (855–1480 m), North Island (670 m).

A species of upper montane forests and the alpine zone. Found creeping among flowering plants at the side of a cascading stream in a *Nothofagus* forest at 855–870 m (near South Branch of Borland Burn, Fiordland Natl. Park). Schuster (1996a) cited a specimen from a moist clay bank in a *N. menziesii* forest, growing mixed with *Paracromastigum furcifolium* and *Isotachis* (track to Hopurahine Falls, Waiotupukura River near Lake Waikaremoana, Urewera Natl. Park, ca. 670 m, *leg. Schuster*). Also occurring at the lip of a grassy area along the side of a seepage area at the margin of a tarn in a mosaic of tussock grass and alpine vegetation along with tarns, rills, rocky outcrops and boulderfields (Rainbow Skifield, St. Arnaud Ra., 1360–1480 m). The type is from Mt. Taranaki.

Comments: We have broadened the concept of this species to include populations that have variable lobe apices, some lobes terminating in a single cell or a uniseriate row of 2 subisodiametric cells, while others are commonly narrowly rounded (e.g., *Engel 18692* from near the South Branch of Borland Burn, Fiordland Natl. Park). Another collection (*Engel 22786* from Rainbow Skifield, Nelson Lakes Natl. Park) has leaf lobes mostly acute and often with a uniseriate row of 2 cells, but also has occasional lobes that are narrowly rounded and appear much like those of the Borland Burn plant. Such populations otherwise have characters typical of the species, i.e., a) deeply bilobed (to 0.7–0.9) leaves that are folded and have a distinct, recurved keel; b) strongly gibbous sinus bases; and c) a markedly papillose leaf surface. It should be emphasized that the shape and form of the leaf lobe apex no longer may be utilized as characters to distinguish *Allisoniella recurva* from *A. nigra* (cf. keys in Schuster, 1972a, 2002a).

The type was sparing and had only immature gynoecia, and, on that basis, the species was stated to be "Dioecious?" by Schuster (1972a). However, based upon study of more abundant plants, Schuster (1996a, p. 12) found the species to be "clearly autoecious."

This taxon differs from all others in *Allisoniella* in the very conspicuously papillose surface (the papillae are readily evident when leaf profiles are examined) and more deeply bifid lateral leaves, usually divided to 0.7–0.9 and only sporadically to 0.6–0.65. The keel is usually concave, in part because the sinus is strongly decurved, and spreads at approximately right angles to the stem or is distinctly decurved. The stems have only a single layer of tangentially somewhat flattened cortical cells delimited; these cells are thick-walled and papillose on the thickened free walls.

The species is similar to the southern South American *Allisoniella subbipartita* (C.Massal.) R.M.Schust. & J.J.Engel in the pointed lobes, often ending in 2 superposed cells, and 1-stratose cortex, but that species has leaves 0.85–0.95 bifid and a smooth or obscurely papillose leaf surface.

Cephaloziella (Spruce) Schiffn., *nom. cons.*

Dichiton Mont., Syll. Gen. Sp. Crypt. 52. 1856, *nom. rej.*

Cephalozia subg. *Cephaloziella* Spruce, Cephalozia 23, 62. 1882. *Cephaloziella* (Spruce) Schiffn. *in* Engler & Prantl, Nat. Pflanzenfam. 1(3): 98. 1893.

Cephalozia subg. *Prionolobus* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 508. 1885. *Prionolobus* (Spruce) Schiffn. *in* Engler & Prantl, Nat. Pflanzenfam. 1(3): 98. 1893.

Lophoziella Douin & Schiffn. *in* Douin, Rev. Bryol. 40: 67. 1913.

Evansia Douin & Schiffn. *in* Douin, Rev. Bryol. 40: 66. 1913; Douin, Bull. Soc. Bot. France 60: 480, 492. 1914 (1913).

Protocephaloziella Douin, Mém. Soc. Bot. France 29: 52, 55. 1920.

Plants straggly, creeping, often as isolated plants amidst coarser bryophytes, sometimes in short tufts, usually deep green to often reddish to brownish to purplish red, in extreme cases piceous or blackish, very small to minute, usually under 350 μm wide with leaves, the leafy shoots sometimes becoming filiform and microphyllous, the plants without a system of basal, leafless axes. Branching sparing, irregular, the branches of lateral- and/or ventral-intercalary type, the branches often elongating indefinitely (if not terminated by a gynoecium); *Frullania*-type branches sometimes present in primitive taxa, *Acromastigum*-type branches very rare. Stems filiform, often sinuous or tortuous, ± wiry, the cortical cells ± firm, not hyaline, like the medullary cells or somewhat thicker-walled, occasionally a little larger. Leaves usually vertical, generally remote (the stems extensively exposed), uniformly bifid to 0.5–0.8, the insertion and orientation transverse (in ours) or in a few taxa succubous, the insertion lines extending to stem midline dorsally, the leaves often loosely folded; lobes ± divergent (when flattened), subequal to equal (rarely with dorsal lobe reduced), mostly narrowly acute to lanceolate, usually only (2)3–9(11) cells wide at base, entire or sometimes toothed, the abaxial surface smooth or in a few species with cellular outgrowths. Cells thin- to more often evenly thick-walled, sometimes strongly so, mostly subquadrate to short-rectangular, small, usually 8–15 μm wide (rarely larger), becoming somewhat larger toward the base; surface smooth to conspicuously papillose. Oil-bodies usually (2)3–9 per cell, finely and obscurely granular and usually appearing almost homogeneous, small, spherical to ovoid. Underleaves small (to 0.35 area of leaves), variable in size and form: lanceolate, as broad as stem and shallowly bilobed, to reduced, few-celled, triangular lamellae to vestigial and consisting of a slime papilla. Gemmae frequent in almost all species, from margins of uppermost malformed and often reduced

leaves (and underleaves) which are dentate-margined, the gemmae 2-celled, elliptical, smooth or sometimes covered with papillae, or angulate.

Dioecious, autoecious or paroecious. Gametangia mostly on elongated leafy shoots, but sometimes ♂ or ♀ (or both) on reduced, few-leaved or leafless intercalary branches. Androecia usually similar in diameter to vegetative sectors or broader, loosely to compactly spicate (in non-paroecious taxa); bracts bilobed, like the leaves except ventricose at base and often more toothed; antheridia usually single per bract, the body ovoid, with cells in 4 irregular tiers, the stalk usually 1-seriate, very rarely 2-seriate. Gynoecia if unfertilized, always innovate, the innovations often indeterminate in length, the gynoecia with bracts and bracteoles in 2–3 series, those of innermost series connate (often strongly) and forming a cup- or urn-like sheath around perianth base (free only in a few species in subg. *Schizophyllum*); bracts similar to leaves except larger and with margins usually dentate (even when vegetative leaves are entire), usually 2-, less often 3-lobed; bracteole unlobed or bilobed, from ca. 0.5× to ca. subequal to bract in size. Perianth usually long-emergent, often ± prismatic, (3)4–5-plicate, somewhat but not greatly contracted to the truncate mouth; mouth often bleached, with cells variously elongated, mostly narrow, thick-walled and entirely or variously in part laterally free, lending the mouth mostly crenulate or, less often, ciliolate (but never long-ciliate).

Seta with 4(5–6) rows of large, swollen outer cells and 4 opposed rows of minute inner cells. Capsule long-exserted, ellipsoidal, the valves thin, 2-stratose; outer layer of cells with a one-phase ontogeny, all or most longitudinal and many transverse walls with well-defined nodular thickenings, the valve base with 4–5 large, swollen cells; inner layer of cells very similar, with similar, often weaker nodular thickenings, sometimes tangentially extended as incomplete to complete bands.

Spores small, 6–12 μm in diam., finely papillose, appearing nearly smooth; spore:elater diam. ratio mostly ca. 1:1. Elaters 2-spiral.

Type: *Cephaloziella divaricata* (Sm.) Schiffn. (≡ *Jungermannia divaricata* Sm.)

"Perhaps no genus of Hepaticae is more difficult than *Cephaloziella*" (Schuster, 1980b, p. 39), with the consequence that it is poorly known taxonomically. The genus includes ca. 90 validly described species and is worldwide in distribution, including presence in both the Arctic (north to ca. 83° N) and the Antarctic. Many of the species were recognized by Douin (e.g., Douin, 1920) in his detailed study of the genus. His studies, however, are of limited use in our understanding of the genus, since his concepts are overly precise, unrealistic and noncritical. Müller (1947, 1951–58) and Schuster (1972a, 1980b, 1996a, 2002a) did much to advance our knowledge of the taxonomy of the group.

The genus is fairly well represented in the Antipodes. The southern South American species are treated in Fulford (1976), but her treatment is of limited value since it is neither complete nor critical. Engel (1978) included three species for the Brunswick Peninsula (Strait of Magellan) (*Cephaloziella dusenii* Steph., *C. gemmata* J.J.Engel and *C. verrucosa* Steph.), and Engel (1990a) recorded one species, *C. dusenii*, for the Falkland Islands. Arnell (1963) treated 12 South African taxa, and Bednarek-Ochyra et al. (2000) treated two species, *C. hispidissima* and *C. varians* for Antarctica. The genus is subdivided into five subgenera and several sections (Schuster 1980b, 1996a). The 17 species present in New Zealand belong to four subgenera: 13 occur in subg. *Cephaloziella*, one in subg. *Schizophyllum*, one in subg. *Evansia*, and one in subg. *Distochopsis*. One species, *C. rufobrunnea* R.M.Schust., is of questionable affinity, even generically, and is not assigned to a subgenus.

Several inherent aspects of the genus make them the most difficult and technical of New Zealand hepatics. They are small to minute in size, frequently sterile, often present either in small quantity or as isolated strands amidst other bryophytes, frequently intimately admixed with another taxon of *Cephaloziella*, and have subtle characters that at times offer difficulties. For example, sexuality is often difficult to determine, even when ♂ and ♀ gametangia are present. Plants are either obviously dioecious (the ♂ and ♀ plants not or only casually admixed), "pseudodioecious" (autoecious, but ♂ and ♀ on long, leafy axes, often so widely separated that connections between the two often decay and plants seem dioecious); or obviously autoecious (♂ and ♀ branches closely associated and juxtaposed, in ours the ♀ often on short branches arising from near the androecial axis) or paroecious. For a detailed account of the methodology and taxonomic problems in the genus, see the treatment of North American taxa in Schuster (1980b).

The treatment below is drawn heavily from Schuster (1972a, 1996a).

References: Douin (1920); Schuster (1972a, 1980b, 1996a, 2002a).

Because the genus is the most difficult and technical of our hepatics, a key to subgenera, after Schuster (2002a), is provided.

Key to subgenera in New Zealand

1a. Gemmae smooth, citron-shaped; leaf lobes normally edentate, but disc near base sometimes with 1–2 strong teeth or denticulations 2
  2a. Shoots at apices subterete, like older sectors; shoot apices not autonomously dorsally assurgent 3
    3a. Gynoecia and androecia all or in part terminal (the androecia eventually intercalary) on leading leafy, elongated stem, the gametangial branches never clustered (in autoecious taxa usually broadly separated); leaves usually 0.4–0.65 bifid; unfertilized gynoecia innovating. Underleaves present or absent . . . . . subg. *Cephaloziella* (p. 586)
    3b. Gynoecia and (sometimes) androecia uniformly on abbreviated ventral-intercalary branches, often clustered and/or juxtaposed; plants always clearly autoecious; leaves 0.65–0.85 bifid; unfertilized gynoecia not innovating. Underleaves always distinct . . . . . subg. *Schizophyllum* (p. 584)
  2b. Shoots distally strongly dorsiventrally compressed, sphenoloboid, the leaves laterally patent, folded. Leaves asymmetrical, the dorsal lobes reduced in size, the ventral margin convex (and ampliate), serrulate; underleaves lacking, not even slime papillae discernable; gemmae and gametangia unknown . . . . . subg. *Distichopsis* (p. 605)
1b. Gemmae covered with coarse, hemispherical papillae; leaf margins and/or bracts, ± strongly spinose-dentate. Underleaves distinct; leaves with lobes similar in shape, both with ± remote, sharp, 1-celled teeth; leaves strongly patent; shoots never conspicuously flattened . . . . . subg. *Evansia* (p. 604)

Key to Species

1a. Underleaves usually conspicuous to small, often readily visible when plant seen in profile. Plants with remote to approximate leaves, never filiform-julaceous; perianth 1-stratose to base (to 2[3]-stratose in *C. muelleriana*) 2

2a. Plants monoecious (autoecious or paroecious), but sometimes pseudodioecious owing to decay of older sectors connecting ♂ and ♀ branches 3

3a. Underleaves small, few-celled, often vestigial; usually pseudodioecious, the elongated ♂ and ♀ branches usually not contiguous; plants rusty- or red-brown, normally on charred, carbonized logs or stumps. Plants slender, remote-leaved; leaf lobes on sterile shoots usually only 4–6 cells wide at base; lobes of ♀ bracts with several spinose teeth . . . . . *C. exiliflora* (p. 595)

3b. Underleaves well developed, lamellate, often bifid, with 1–2 or more teeth; clearly autoecious, the connections between ♂ and ♀ branches usually obvious, or paroecious; plants confined to peat, soil or rocks 4

4a. Plants paroecious: antheridia in axils of 1–2 cycles of large, concave bracts below ♀ bracts; ♀ bracts and subfloral leaves hyaline-margined, with sharply differentiated border (cells within with reddish or red-brown walls); perianth, below bleached apex, ± strongly reddish pigmented . . . . . *C. nothogena* (p. 594)

4b. Plants clearly autoecious: antheridia in axils of relatively small but concave bracts in separate, spicate androecia; ♀ bracts and subgynoecial leaves without a sharply defined hyaline border; perianth and/or leaves without reddish pigments 5

5a. ♂ and ♀ Branches never short and clustered, often elongated, sometimes widely spaced (then pseudodioecious); plants less vigorous, under 350 μm wide with leaves (or stem armed), never helophytic; ♀ bracts free from bracteoles or almost so, their lobes spinose-dentate or subentire; perianth mouth crenulate or crenulate-setulose, with cells 2–4:1. Stems with cellular processes in some species 6

6a. Stems smooth; abaxial face of leaf smooth (or a little mamillate near ♀ bracts), never armed; ♀ bracts with lobes entire or subentire; leaf and underleaf margins edentate, their tips never with elongated cells, usually blunt; plants usually locally vinaceous or purplish pigmented . . . . . *C. varians* (p. 600)

6b. Stems armed with sharp, 1–3-celled (rarely ramified) processes; abaxial face of leaf below lobes armed with cellular processes; ♀ bracts with ± sharply toothed lobes; leaf and underleaf margins denticulate or dentate, at least in basal half, their lobe tips often formed of 1–2 elongated cells (but sometimes blunt); plants grey-green, with cell walls pigment free . . . . . *C. hispidissima* (p. 589)

5b. ♂ and ♀ Branches clustered in groups of 2–5, the ♂ often on leading shoot, with short ventral-intercalary ♀ branches and androecia juxtaposed; plants vigorous, to 350–400(500) μm wide, helophytic; ♀ bracts and bracteole conspicuously connate, their lobes spinose-serrulate; perianth mouth denticulate, with cells 4–8:1. Stems lacking cellular processes . . . . . *C. pulcherrima* (p. 584)

2b. Plants dioecious (very often sterile), the ♂ and ♀ shoots usually in separate patches. Underleaves usually large; stem never armed; leaves sometimes denticulate or dentate 7

7a. Leaf margins entire (or if sparingly and irregularly dentate or denticulate then the teeth never ending in a firm-walled tubercle); leaves on non-gemmiferous plants, if toothed, with abaxial leaf surface usually armed; cells of leaf ± uniform in size; plants locally rose-red to purplish, never with warm brown pigments; gemmae smooth, ellipsoidal 8

8a. Cells at lobe bases 10–13 × 12–15 μm up to 15–17 × 17–19 μm; plants relatively tiny, the shoots with leaves 200–300(350) μm wide; leaves bilobed to 0.55–0.7, the lobes ending in 1 or 1(2) non-elongated cells; oil-bodies (?*C. muelleriana*) (1)2–5(6) per cell 9

9a. ♀ Bracts irregularly, usually weakly denticulate, the lobe apices never hooked; perianth-mouth cells ca. 2–4:1, with the lumina never reduced to vestiges; leaves mostly little wider than stem, the latter stout (usually over 150 μm in diam.), with lobes usually 6–9 cells broad at base, the sinus sharply angular. Cells at lobe bases 10–13 × 12–15 μm, verrucose; oil-bodies (1)2–3(5) per cell, faintly granular . . . . . *C. byssacea* (p. 587)

9b. ♀ Bracts conspicuously serrulate or denticulate-serrulate, the lobe tips often hooked; perianth-mouth cells linear, ca. 6–9(10):1, very thick-walled; leaves ± spreading, wider than stem, the latter slender (usually 75–110 μm in diam.), with lobes 4–5 or 6–10 cells broad at base, the sinus sharp to rounded 10

10a. Leaf lobes (7)8–9(10) cells broad, entire-margined, the disc margins also unarmed; sinus obtuse to sharp, angular; ♀ bracts very regularly, sharply serrulate, the lobe cells very thick-walled and mostly linear or sublinear; ♀ bracts conspicuously serrulate. Perianth-mouth cells with lumina largely obliterated, the walls very thick; cells at lobe bases 14–18 μm wide. ?Oil-bodies . . . . *C. muelleriana* (p. 590)

10b. Leaf lobes 4–5(6) cells broad on sterile shoots, sporadically with 1–2 weak, 1-celled teeth of lobe bases or disc; sinus blunt to rounded at base; ♀ bracts weakly, less closely, less regularly serrulate, the lobe cells feebly thick-walled, with oblong, angular lumina; cells at lobe bases 11–14 μm wide; ♂ bracts with lobes edentate. Oil-bodies minute, 1–1.6 μm in diam., usually 3–6 per cell, homogeneous and smooth . . . . . *C. invisa* (p. 591)

8b. Cells at lobe bases 14–19(21) μm wide; plants vigorous, to 400 μm wide with leaves; leaves bifid to 0.7–0.8, the lobes ending in 1–2(3) somewhat elongated cells; oil-bodies 8–12 per cell. Leaf lobes incurved, 8–11(14) cells broad . . . . . *C. grandiretis* (p. 593)

7b. Leaf margins loosely on mature axes dentate-serrate with ± sharp teeth, the coarser teeth ending in a sharp, thick-walled tubercle; leaves with abaxial surface always smooth; cells in leaf apices and peripheral sectors small, abruptly larger at lobe bases and in disc; plants light green, but exposed sectors ± warm brown pigmented; gemmae polygonal-stellate. Cells at lobe bases 15–19 μm wide within margins; lobes broadly triangular, rather short, 6–9(10) cells broad at base . . . . . *C. subspinosa* (p. 604)

1b. Underleaves lacking on sterile and gemmae-free shoot sectors or a mere 1-celled papilla or (rarely) a 2-celled spur, never developing a lamina. Cell surfaces with low but distinct papillae (except *C. exigua* and *C. rufobrunnea*); oil-bodies (where known) (0)1–3(4) per cell 11

11a. Leaves of sterile shoots usually symmetrically or subsymmetrically bilobed, edentate (except *C. exigua*) never folded; shoot apices terete, not upcurved; autoecious or pseudodioecious (sexuality unknown in *C. rufobrunnea*) 12

12a. Shoots at maturity hyaline (leaves decolorate, difficult to resolve) but shoot apices with leaves, locally at least, intensely vinaceous or bright reddish pigmented; leaf cells at maturity very thick-walled, with guttulate lumina. Sterile or dioecious 13

13a. Cells densely covered with hemispherical coarse papillae; leaves imbricate, with little or no stem visible in lateral view; leaf lobes edentate; plants alpine . . . . . *C. aenigmatica* (p. 586)

13b. Cells smooth; leaves remote, with much of stem visible; leaf lobes serrulate-crenulate with thick-walled tips of projecting cells; plants lowland . . . . . *C. exigua* (p. 603)

12b. Shoots not hyaline, the leaves not becoming decolorate, the shoot apices never bright red or vinaceous; leaf cells never guttulate. Autoecious or pseudodioecious 14

14a. Leaves remote to contiguous, not clearly folded; lobes flat or adaxially concave 15

15a. Plants olive-green to blackish, without trace of reddish pigments; leaf lobes ± unequal; perianth 4–5-stratose (to 65 μm thick) in basal 0.25, 1–2-stratose medially, the mouth crenulate-denticulate with cells 1.5–3(4):1 . . . . . *C. crassigyna* (p. 597)

15b. Plants light clear translucent green and with exposed sectors rusty red or (*C. rufobrunnea*) rusty red-brown throughout; leaf lobes equal; perianth (known only for *C. pseudocrassigyna*) 1-stratose to base, the mouth setulose with cells usually 4–5.5:1, free at their tapered, narrow, thick-walled apices 16

16a. Plants light clear translucent green, with exposed sectors rusty red; hygrophytic, growing along rills . . . . . *C. pseudocrassigyna* (p. 600)

16b. Plants rusty red-brown throughout; xerophytic, growing in exposed, difficult sites . . . . . *C. rufobrunnea* (p. 607)

14b. Leaves densely imbricate, ± folded, the sinus bases tending to be folded downward; lobes abaxially concave, at least the dorsal margins elevated and/or reflexed. Ventral-intercalary stolons occasional . . . . . *C. densifolia* (p. 598)

11b. Leaves of sterile shoots quite asymmetrically bilobed (ventral half larger, with ampliate basal sector, clearly crenulate-denticulate), at shoot apices leaves ± complanate; shoot apices flattened, the tips upcurved; sterile, presumably dioecious. Shoots pellucid, whitish, except for some shoot tips with weak purplish brown pigmentation . . . . . *C. pellucida* (p. 605)

Subg. ***Schizophyllum*** Müll.Frib.

Cephaloziella subg. *Schizophyllum* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland, ed. 2, 6(2): 113. 1912. *Cephaloziella* sect. *Schizophyllum* (Müll.Frib.) Jörg., Bergens Mus. Skr. 16: 188. 1934. Lectotype: *C. elachista* (Jack) Schiffn.

Branching exclusively intercalary, usually all ventral. Gemmae ellipsoidal or citron-shaped. Autoecious (normally), with ♂ and ♀ normally juxtaposed, the gynoecia on short intercalary branches from leading shoots and adjacent androecia on leading leafy axes, or gynoecia terminal on leafy axes, with adjacent spicate ♂ branches.

Cephaloziella pulcherrima R.M.Schust.

Cephaloziella pulcherrima R.M.Schust., Nova Hedwigia 22: 203. *f. 20: 4–7; 21.* 1972 (1971). Holotype: New Zealand, South Is., Fiordland Natl. Park, track from Lake MacKenzie to Harris Saddle, ca. 3800 ft., *Schuster 67-369.*

Plants creeping to decumbent, whitish to light green, upper portions (especially median sectors of perianths, nonmarginal sectors of ♀ bracts) rose-red to intense red, relatively vigorous, the leafy shoots 250–400(500) μm wide × 12–25 mm long (150–290[320] μm wide in subsp. *sphagnicola*). Branching sporadic, irregular, the branches ventral-intercalary. Stems firm, rather thick, ca. 8–9 cells high, the cortex in 1–2 layers of smaller, quite thick-walled cells, in surface view striolate; medullary cells firm but thinner-walled. Rhizoids frequent, colorless. Leaves vertical, suberect, remote, quite concave but not folded, transverse, inserted to stem midline dorsally, oblong to oblong-obtrapezoidal, ca. 200–250 μm wide × 250–310 μm long, bifid to 0.65(0.8); lobes linear-lanceolate, 6–8 cells broad at base, the lobe apices acuminate and almost invariably uncinate at tip, terminating in a single cell or a uniseriate row of 2(3) elongated hyaline cells, the terminal cell 12–14 × 30–38 μm; leaf margins edentate to vaguely sinuous-dentate, the disc margins entire or occasionally with a small, single tooth that is oblique to erect, never spreading. Abaxial face of leaf usually smooth, very rarely an isolated leaf with a few mammillae or blunt, 1-celled abaxial projections of disc (freely armed in subsp. *sphagnicola*). Cells rather large, at lobe bases 15–19 μm wide × 24–31 μm long; cell surfaces with numerous medium large, often contiguous, conspicuous papillae. Oil-bodies (Schuster, 1972a) almost homogeneous, glistening, ovoid to spherical, (2)3–6(9) per cell, 3–4 μm to 3–4 × 5–6 μm, rarely 4.8 × 6 μm, not or little larger than chloroplasts. Underleaves present throughout, medium to large, 70–90 × 165–200 μm to 135 × 300 μm, irregular in shape, often asymmetrically bifid to 0.2–0.6, the margins below often with 1–2 teeth; abaxial face usually smooth. Gemmae lacking.

Autoecious, abundantly fertile. Androecia usually terminal on leading shoots, with (1)2–3(4) juxtaposed ventral-intercalary, short gynoecial branches developed from near their base, the gametangia thus clustered and autoecious inflorescence always obvious (gametangial branches not clustered in subsp. *sphagnicola*); bracts in ca. 3–7 pairs, densely imbricate, the androecium compactly spicate. Gynoecial bracts connate with each other, the bracteole connate on both sides for 0.25–0.35(0.45), forming a tight adherent cup around perianth base, only the lobes erect-spreading; bracts and bracteole ± similar in size and form, 2–3-lobed to 0.4(0.5), the lobes of bracts and bracteoles lanceolate-acuminate, the slender tips usually falcate, the margins sharply serrulate, with apices terminating in 1–2 strongly elongated cells

(12–14 × 50–55 μm), the lobe bases often paucispinose with long, 1-celled teeth; non-marginal cells in distal parts of lobes strikingly elongated, 10–12(14) × 35–48(56) μm (ca. 3–5:1), thick-walled, papillose. Perianth large, bluntly but deeply trigonous in distal half, decolorate at mouth and usually at base, rose-red to deep purplish red between; mouth and area immediately below formed of strikingly elongated cells in contrast to the short-oblong ones lying below, the mouth shallowly lobulate and irregularly crenulate-setulose, with the tapered free tips of the thick-walled apical cells.

Seta with 4–5 very large epidermal cell rows and 4–5 minute, internal cell rows. Capsule with base of each valve formed of 5–6 large, swollen hyaline cells, each longitudinally subdivided by a vertical wall bearing nodular brown thickenings; outer layer of cells oblong, most but not all longitudinal walls with brownish, rather small, remote, well-defined, nodular thickenings, the transverse walls rarely or occasionally with 4–6 small nodular thickenings per wall; inner layer of cells generally with complete to incomplete semiannular bands or (often) nodular thickenings with ± short tangential extensions.

Spores brownish, 8.5–9.5 μm in diam., densely and sharply papillose-vermiculate. Elaters 7–8 μm wide, 2-spiral (medially occasionally 3-spiral).

Comments: *Cephaloziella pulcherrima* may be readily distinguished from all other New Zealand species of the genus because it bears gynoecia always on abbreviated ventral-intercalary branches which usually arise very close to androecia. The latter are typically on long leafy axes. On this account, the autoecious condition is readily evident.

This vigorous species is unrelated to other Australasian taxa, but rather is allied to the *Cephaloziella elachista–spinigera* complex of Arctic-subarctic to cold-temperate loci (Schuster, 1980b, 1988). Unlike the members of that complex, the ♀ bracts are conspicuously fused with the bracteole (forming a basal sheath) and the perianth mouth is denticulate to ciliolate. Also, the disc margins of the leaves lack the spreading to squarrose spinose teeth found in the *C. elachista–spinigera* complex.

Cephaloziella pulcherrima is divisible into two subspecies, as follows.

Key to Subspecies

1a. ♂ and ♀ Branches clustered in groups of 2–5; abaxial surface of leaves usually smooth; cells of perianth mouth more elongate, 42–66 μm long; leafy shoots 250–400(500) μm wide . . . . . subsp. *pulcherrima* (p. 585)

1b. ♂ and ♀ Branches not clustered; abaxial surface of leaves freely armed; cells of perianth mouth somewhat less elongate, 28–41(48) μm; leafy shoots 150–290(320) μm wide . . . . . subsp. *sphagnicola* (p. 586)

Cephaloziella pulcherrima R.M.Schust. subsp. ***pulcherrima***

Leafy shoots 250–400(500) μm wide; abaxial surface of leaves usually smooth; gametangial branches clustered in groups of 2–5; cells of perianth mouth 42–66 μm long.

Distribution and Ecology: Endemic to New Zealand: South Island (730–1160 m). Known from Fiordland (Humboldt Mtns.), Otago (Swampy Hill) and Westland (Otira River valley) EPs.

A helophytic taxon, occurring in open, swampy or boggy sites, sometimes on the less hygric margins of peat-edged tarns (type), sometimes on saturated peaty ground. In the upper Otira valley it was found on damp peat soil with *Dicranoloma robustum* in *Dracophyllum rosmarinifolium – Chionochloa rubra* tussockland on the valley floor.

Cephaloziella pulcherrima subsp. ***sphagnicola*** R.M.Schust.

Cephaloziella pulcherrima subsp. *sphagnicola* R.M.Schust., Nova Hedwigia 22: 205. *f. 22*. 1972 (1971). Holotype: Tasmania, Lake St. Clair Natl. Park, Mt. Rufus, NW of Derwent Bridge, 4500–4750 ft., *Schuster 50541*.

Leafy shoots 150–290(320) μm wide; abaxial surface of leaves freely armed; gametangial branches not clustered; cells of perianth mouth 28–41(48) μm.

Distribution and Ecology: New Zealand: South Island (390–1100 m). Also known from Tasmania.

In New Zealand known from Western Nelson (Cobb Valley) and Westland (Maruia River valley near Reids Stream, St. Arnaud) EPs.

Found on mounds of *Sphagnum cristatum* in *Sphagnum* bogs with varying amounts of *Empodisma minus* and *Chionochloa rubra*, surrounded by *Nothofagus solandri* var. *cliffortioides* forest.

Subg. ***Cephaloziella***

Leaves (in our taxa) with the lobes edentate, or sporadically with a few teeth associated with gemma formation, then teeth irregular and jagged. Stem usually with a weakly to well-defined 1-layered cortex of smaller, thicker-walled cells. Gemmae citron-shaped or ellipsoidal, 2-celled, smooth.

All our species of this subgenus agree in that leaf lobe margins are edentate, unless with prolonged gemmae formation they become irregularly toothed and somewhat ragged.

Cephaloziella aenigmata R.M.Schust.

Cephaloziella aenigmata R.M.Schust., Nova Hedwigia 63: 20. *f. 2*. 1996. Holotype: New Zealand, South Is., Paparoa Ra., NE of Mt. Euclid, 3800–4300 ft., *Schuster 84-1577*.

Plants creeping amidst other hepatics, usually as isolated plants or somewhat gregarious, whitish, decolorate, translucent to transparent, the stem readily visible through the hyaline bleached mature leaves, only the distal leafy shoot sectors sporadically brownish purple to reddish purple or vinaceous; plants small, the leafy shoots 150–250 μm wide, to 6 mm long, the leafy axes sporadically becoming flagelliform and microphyllous. Branching sparing and irregular, the branches chiefly (?all) lateral-intercalary; stoloniform, microphyllous, geotropic axes sparingly produced, originating from ventral face of stem, colorless. Rhizoids colorless, infrequent, absent or nearly so on normal-leaved axes. Stems wiry and rigid, colorless above, pale brownish with age, with gradual transition from an exceedingly thick-walled outer cortical

layer (lumina small, round or oval, free walls exceptionally thick) to a somewhat larger-celled hyaline medulla formed of moderately incrassate cells, a leptodermous central medulla lacking. Leaves stiffly, pectinately distichous, usually obliquely suberect (the lamina obliquely spreading, the lobes erect or suberect), the leaves, *in situ*, with the dorsal margin often feebly recurved, the leaves exceptionally densely imbricate (stem, in dorsal view of shoots, wholly hidden), transversely inserted and oriented, the leaves (flattened) subquadrate, ca. 180–200 × 180–210 μm, symmetrically bilobed to 0.55–0.75; lobes narrowly, acutely triangular, with straight or feebly arched sides, (7)8–11(12) cells broad at base, terminating in a single cell or often a uniseriate row of 2 cells, the apical cells subisodiametric (usually as broad as long) or weakly elongated, tapering to an acute summit, the tips never beaked; margins edentate or isolated leaves with a solitary tooth on ventral margin, but appearing ± finely crenulate because of the tubercle-like marginal swellings of the radial cell walls (swollen septa); sinus acute, *in situ* often with lobe margins somewhat recurved. Cells strongly thick-walled, often guttulate, the lumina rounded (especially so near ventral leaf bases, where cells are hyaline, exceptionally thick-walled); marginal cells rounded-subquadrate, only (7)8–11 × 8–12 μm; intramarginal cells in lobe bases somewhat larger, 10–12 × 15–20 μm to 12 × 12–14 μm, usually clearly larger and mostly longer than marginal cells; cell surfaces usually very coarsely papillose, the papillae dome-like, diverse in size, usually contiguous in and near lobe apices. Oilbodies (Schuster, 1996a) (1)2–3 per lobe cell, smooth (and hardly perceptibly granular), small, not or hardly larger than chloroplasts, ca. 2.5 × 3.5 μm. Underleaves lacking. Asexual reproduction by colorless (when young), ellipsoidal or ovoid, smooth, 2-celled gemmae, ca. 7–8 × 13–15 μm.

?Dioecious. Androecia unknown. Gynoecia (only immature known) on elongated or ± abbreviated axes, with 2–3 gyres of progressively larger bracts, the innermost rounded-quadrate, bilobed to ca. 0.4–0.5, the lobes acute, entire, the disc sometimes with a blunt tooth below; bracteole free from bracts, small. Perianth (only very juvenile known) pluriplicate, the mouth lobulate-ciliolate, some cilia 1–2-celled, of long cells (6.5–8 × 18–20 μm to 6–7 × 21–30 μm) their tips narrowed, acute.

Distribution and Ecology: Endemic to New Zealand: South Island (1160–1310 m). Known only from the type, which occurred mixed with *Nothogymnomitrion erosum*, *Radula sainsburiana*, *Cheilolejeunea albovirens*, *Paraschistochila conchophylla*, *Jamesoniella* and the filmy fern *Hymenophyllum armstrongii* over a damp rock wall in a thicket of *Nothofagus menziesii – Dracophyllum traversii* in the otherwise penalpine zone.

Comments: The leaves are unusually densely imbricate for the genus, and little or no stem is visible in lateral view. The species is also unusual in that the mature shoots have decolorate leaves and the stem is readily visible through the ± hyaline leaves; only the shoot apices are reddish pigmented. Leaf cells are notably thick-walled, with a guttulate lumina, and the surface is densely covered with hemispherical coarse papillae.

Cephaloziella byssacea (Roth) Warnst.[1]

Jungermannia byssacea Roth, Tent. Fl. Germ. 3: 307. 1799. *Cephalozia byssacea* (Roth) Dumort., Recueil Observ. Jungerm. 18. 1835. *Cephaloziella byssacea* (Roth) Warnst., Krypt.-Fl. Brandenburg 1: 224. 1902. Type: Germany (W!, herb. Lindenberg).

[1]For additional synonymy see Schuster (1980b, pp. 85–86).

Jungermannia confervoides Raddi, Jungermanniogr. Etrusca 18. 1818; Mém. Soc. Ital. Sci. Modena 18: 29. 1818. Type: Italy.

Jungermannia starkei Funck *ex* Nees, Naturgesch. Eur. Leberm. 2: 223. 1836, *nom. illeg.* *Cephaloziella starkei* (Funck *ex* Nees) Schiffn., Lotos 48: 341. 1900, *nom. illeg.* Type: Germany.

Jungermannia divaricata Sm. *in* Sowerby, Engl. Bot. 10: 719. 1800. *Cephalozia divaricata* (Sm.) Dumort., Hep. Eur. 89. 1874. *Cephaloziella divaricata* (Sm.) Schiffn. *in* Engler & Prantl, Nat. Pflanzenfam. 1 3(1): 99. 1893. Type: Great Britain, Norfolk, *Francis*.

Plants filiform and often rather rigid, brittle, commonly loosely decumbent (or, when crowded, erect), scattered or in loose patches, green or ± brown to (usually) locally purplish brown or copper-red to vinaceous, occasionally blackish, the shoots 160–450 μm wide. Branching remote, the branches usually intercalary, lateral, and ventral (rarely terminal and *Frullania* type); often with subfloral innovations. Stems relatively stout, the cortical cells in surface view quadrate to short-rectangular, in cross section with walls somewhat to strongly thickened, the cell lumina often guttulate and rounded. Rhizoids sparsely developed. Leaves strongly rose-red to purplish red pigmented, with base usually ± spreading on mature plants or erect-spreading, but lobes loosely (sometimes abruptly) folded upward and erect or suberect, folded in vigorous phases, remote, transversely inserted and oriented, broadly quadrate to obtrapezoidal, small, commonly little broader than stem, bilobed to 0.5–0.65; lobes ovate-triangular to ovate-lanceolate, acute or subacute, terminating in 1 cell or a uniseriate row of 2 subisodiametric cells, on mature sterile shoots (5)6–9(10) cells broad at base, entire or with a small basal tooth; sinus often slightly reflexed. Cells copper-red to purplish, thin to slightly thickened, occasionally prominently thick-walled, (8)9–12(13) μm wide × 12–15 μm long at lobe bases (in ours); cell surfaces smooth or (less often) weakly papillose. Oil-bodies (Schuster, 1972a, 1996a) in ours (1)2–3(5) per cell, faintly granular, rather large, 3–3.5 × 3.5 to 4–4.5 × 5–5.5 μm. Underleaves of mature, sterile, non-gemmiparous shoots usually distinct throughout, rarely obsolete locally, very variable in size, usually lanceolate or subulate, 6–9(10) to 15–17(19) cells wide at base (in ours). Gemmae often present, green to (sun forms) usually purplish, 2-celled, elliptical with a terminal mamillate projection on each end, ca. 10–15 × 15–25 μm; gemmiparous leaves becoming strongly erose.

Dioecious; commonly sterile, but rather often with plants of the two sexes in separate patches. Androecia often purplish red, becoming intercalary on usually long leafy axes, as wide as vegetative portions of shoots or slightly wider, compactly and usually longly spicate, prominent; bracts strongly concave at base, 0.5 bilobed, the lobes subentire to entire, 1-androus. Gynoecia terminal on long leafy shoots; bracts often purplish red but hyaline at margins and apex, much larger than leaves, 0.3–0.4 bilobed, the lobes subacute or acute to shortly acuminate, denticulate or serrulate to spinulose-dentate with sharply projecting 1(2)-celled spreading teeth; bracteole as long as bracts but usually narrower, similarly lobed and dentate, united with one or both bracts for up to 0.5 its length. Perianth green at base, varying to purplish or reddish purple medially, decolorate at mouth, fusiform-ovoid, ca. 0.5–0.65 emergent at maturity, usually obtusely 4-plicate in distal 0.5–0.6, gradually narrowed to mouth; mouth crenulate with narrow cells.

Spores 6–9 μm in diam., virtually smooth. Elaters 6–8 μm wide.

Distribution and Ecology: New Zealand: South Island (1525–1585 m). Exceedingly widely distributed in the Northern Hemisphere in temperate, boreal and Arctic regions (Schuster, 1980b). The species also occurs in Brazil, Argentina, Colombia and Venezuela (Schuster, 1980b, p. 88). Reports from the Falkland Islands are based on a specimen that is actually

Cephaloziella dusenii (see Engel, 1990a). Extra–New Zealand reports from southern temperate and subantarctic regions require confirmation.

On the flanks of Mt. Brewster (Westland EP) at 1370–1585 m on thin peaty soil over insolated exposed small ledges, where kept moist by seepage and associated with *Marsupella sparsifolia*, *Diplophyllum verrucosum*, *Adelanthus occlusus*, *Lepidolaena taylorii*, *Andrewsianthus* "*confusus*," and *Radula* sp. (Schuster, 1973).

Comments: This highly variable species is unisexual and very often sterile. Underleaves are usually distinct throughout, lanceolate or subulate, and are up to 15–17(19) cells wide at the base. Leaves are strongly rose-red to purplish red pigmented with lobes (5)6–9(10) cells broad at the base, with cells at the lobe bases (8)9–12(13) μm wide × 12–15 μm long.

Cephaloziella hispidissima R.M.Schust.

Cephaloziella hispidissima R.M.Schust., Nova Hedwigia 22: 208. *pl. 23*. 1972 (1971). Holotype: Argentina, Tierra del Fuego, Cerro Garibaldi, SE of Lago Escondido, near Rte. 3 between Ushuaia and Río Grande, ca. 950 m, *Schuster 58304*.

Plants rather rigid and wiry, brittle, creeping to ascending, grey- to olive-green, devoid of wall pigmentation, dull, vigorous, to 640 μm wide with leaves. Branching irregular, the branches strictly ventral-intercalary. Stems (except on weak axes) hispid with sharp, 1–2(3)-celled processes, each with a sharp terminal cell with ± thickened apex, the cortical cells ± non-chlorophyllous, undifferentiated; medullary cells strongly chlorophyllous. Rhizoids scattered, rare. Leaves obliquely to widely spreading, subcontiguous to contiguous, the insertion transverse, extending to stem midline dorsally, mostly loosely conduplicate, with widely spreading keel, often gibbous, 180–230 μm wide × 165–210 μm long, bifid to 0.65–0.75; lobes widely spreading, ± adaxially convex (then weakly canaliculate), ovate to ovate-triangular, 10–12 to 16–18(20) cells broad at base, the tips mostly acute to apiculate, often terminating in a single cell or 2 ± elongated cells, the lobe margins (except on weak plants) usually denticulate varying to sharply few-dentate; disc often with 1–several sharp basal teeth. Abaxial face of leaf usually armed with projecting cells or hispid with cellular processes. Cells at lobe bases weakly thick-walled with angular lumina to thick-walled with guttulate lumina at least in upper parts of lobes, 9–12 μm wide × 11–15(18) μm long. Underleaves large, as broad or broader than the stem, mostly ovate or ovate-lanceolate or oblong, varying to bifid and almost leaf-like, serrulate to irregularly dentate distally, bluntly or sharply pointed, the bases or flanks often with teeth and/or a lacinium on each side. Gemmae at times lacking, when present ovate, smooth, 2-celled, formed on lobe margins of some apical leaves.

Autoecious. Androecia ventral- and ?lateral-intercalary in origin, spicate; bracts leaf-like, more concave basally and not folded. Gynoecia terminating main axes; bracts leaf-like, the lobes 9–12 cells broad, usually more drawn out and acuminate than those of leaves, remotely spinose-dentate with sharp, usually 1-celled teeth, often terminating in a uniseriate row of 2 elongated cells. Perianth 4–5-plicate, the mouth rather wide, crenulate-setulose.

Sporophyte unknown.

Distribution and Ecology: New Zealand: South Island (ca. 1615 m). Amphi-Pacific in world distribution: also known from southern South America (type) and Antarctica (South Orkney and South Shetland islands).

In New Zealand Schuster (1972a) recorded the species from ca. 1615 m in the Old Man Ra. (South Island, Otago), over damp, peaty soil between mosses along a small rill and admixed with *Cephalozia ?australis*.

Comments: A distinctive species in several respects, especially in development of armature. Leaf and underleaf margins are denticulate or dentate, at least in the basal half, and the ♀ bract lobes are sharply toothed. The abaxial face of the leaf below the lobes is armed with cellular processes and the stems are armed with sharp, 1–3-celled processes. Plants are grey-green and secondary pigments are not developed. Also, the stem cortical cells are non-chlorophyllous or nearly so, while the medullary cells are strongly chlorophyllous. Underleaves are present throughout and conspicuous.

Cephaloziella muelleriana R.M.Schust.

Cephaloziella muelleriana R.M.Schust., Nova Hedwigia 63: 24. *f. 3, 4*. 1996. Holotype: New Zealand, North Is., along Whirinaki River, *Schuster 95-371*.

Plants in interwoven small, gregarious patches, or solitary amidst small acrocarpous mosses, minute, with sterile shoots 300–335 μm broad. Branching irregular, the branches ventral-intercalary and at least sporadically, lateral-intercalary; terminal branches unknown. Stems relatively flimsy, 5–6 cells in diam. on weak shoots, 7–8 on vigorous shoots, the cortical cells in an ill-defined, non-pigmented, only weakly to moderately thick-walled layer, in surface view conspicuously striolate; medullary cells feebly firm-walled, with rounded angles, the peripheral stratum at times smaller. Rhizoids scattered, rather frequent even to gynoecial region. Leaves obliquely spreading, remote, transverse, vigorous ones usually loosely folded, evident chiefly at sinus bases, the leaves when flattened narrowly obtrapezoidal in outline, 235–245 μm wide × 180–200 μm long to 260–265 μm wide above × 225–260 μm long, bilobed to 0.5–0.6; lobes narrowly triangular, (7)8–9(10) cells broad at base, entire-margined, ending in 1 or 2 single cells that are not elongated but on vigorous, sterile shoots often somewhat incurved at the tips; sinus rectangular to obtuse-angular on flattened leaves, often rounded at base, on vigorous leaves sometimes somewhat recurved or gibbous and sometimes obscurely armed with a blunt projection just proximal to sinus bases; abaxial surface of lower parts of leaves sometimes obscurely mamillose. Cells rather variable, firm-walled and with rounded angles, the lumina often rounded, at lobe bases 14–18 μm wide × 16–19 μm long; surface conspicuously, rather closely papillose distally, becoming striolate basally. Underleaves distinct on sterile shoots, somewhat spreading, ovate-lanceolate to sporadically bidentate or bifid. Gemmae lacking.

Dioecious. Androecia on long, leafy axes, becoming intercalary, sometimes the apical innovation again androecial after developing only 2–3 gyres of leaves, the androecia compactly and rather smoothly spicate; bracts in 5–7 pairs, closely imbricate, concave, the lobes erect, narrowly triangular, serrulate, sharp-pointed. Gynoecia usually on intercalary branches of limited length, often developing only (1)2–3 gyres of leaves and underleaves prior to initiation of bracts; bracts in 2–3 gradually larger series, the innermost and those of penultimate series bifid to 0.35, the sharp, triangular lobes regularly and sharply serrulate with strongly projecting, thick-walled upper ends of marginal cells; lobe apices mostly abruptly hooked, the hook usually formed of a single, long-acute, thick-walled, tapered, terminal cell; bracts of innermost series 2(3)-lobed to 0.25–0.35, the acute to subacuminate lobes strongly serrulate, the lobes

and margins usually broadly decolorate, hyaline, the cells of lobes formed of very strongly thick-walled and elongated cells; bracteole broadly connate with bracts on both sides, narrower and somewhat shorter than bracts, bilobed to 0.25, the lobes like those of bracts. Perianth 470–525 μm diam. × 850–925 μm long, up to 540 μm diam. × 1650–1900 μm long, slenderly ovoid-ellipsoidal, deeply 3–4-plicate in distal third, narrowed in the distal 0.25–0.35 into a rather narrow mouth; mouth decolorate and bleached, formed of exceedingly thick-walled and strongly elongated cells in the distal 0.1–0.2, below of brownish pigmented, chlorophyllose short-oblong cells; mouth fringed with linear cells (6.5–9:1), 9–11 μm wide × 52–72 μm long, free at the very apices and projecting as thick-walled crenulations; perianth unistratose virtually to base, but at the very base becoming a little fleshy and (2)3-stratose.

Seta formed of 4 rows of inflated, very large outer cells and 4 rows of minute internal cells. Capsule ellipsoidal, purplish brown, with a basal "shoulder" formed of inflated cells in a single tier, the walls 2-layered; outer layer of cells mostly oblong, the longitudinal walls with conspicuous radial nodular thickenings, often opposed, not or scarcely ever confluent; base of each valve with a "cushion" of 8–9 cells, arranged in a fan-like pattern, narrowed basally, broadened distally, 70–80 μm long, the radial walls with remote, minute, radial nodular thickenings; inner layer of cells more variable in size, shape, and thickening patterns, with very small, well-separated, radial nodular thickenings, the thickenings not extended onto tangential walls on some cells, feebly extended on others, on many as an incomplete to complete narrow band, the thickenings then semiannular.

Spores 10.5–12 μm in diam., purplish brown, delicately verruculose. Elaters hardly tapered or tortuous, 7–7.5 μm diam., 2-spiral, the spirals well defined, 2.2–2.4 μm wide.

Distribution and Ecology: Endemic to New Zealand: North Island (380 m).

Known, to date, only from the type collection, on exposed mineral soil of an exposed sandy-gritty bank, and growing amidst small acrocarpous mosses, mixed with *Cephaloziella subspinosa*.

Comments: *Cephaloziella muelleriana* may be distinguished from *C. byssacea*, another dioecious species, by a number of features, among them the ♀ bract lobes and often also the subgynoecial bracts are notably sharply and closely serrulate by thick-walled projections of the walls of the marginal cells, and the strikingly elongated perianth-mouth cells with walls so markedly and massively thickened that the lumina is nearly obliterated and often vestigial. The highly differentiated cells at the perianth mouth are unique in the genus.

Cephaloziella invisa R.M.Schust.

Cephaloziella invisa R.M.Schust., Nova Hedwigia 63: 30. *f. 5, 6*. 1996. Holotype: New Zealand, North Is., Otupaka Frost Flats on South Road, SSW of Minginui, *Schuster 95-386*.

Plants very slender, pale brownish, with tips of actively growing shoots very locally with a little deep purplish pigmentation, minute, the sterile leafy shoots only 240–330 μm wide. Branching rather sparing and irregular, the branches (apparently) all ventral-intercalary, soon acquiring the vigor of the parent shoot. Stems wiry, somewhat brittle, very slender, pale brownish with age, relatively pellucid, the cortex of sterile shoots in 1 layer of only ca. 16 cell rows of subisodiametric cells, in surface view mostly subquadrate; medulla of only 11–14 rows, the walls as thick as those of cortical cells or almost so. Rhizoids scattered, long, frequent. Leaves on sterile shoots erect-spreading to moderately widely spreading, always ex-

ceedingly remote, transversely oriented but insertion lines feebly succubous, mostly moderately concave but never folded, the lobe apices usually incurved, *in situ* sometimes weakly connivent, the leaves (on sterile shoots when flattened) narrowly obtrapezoidal, 135–165(175) μm wide × 125–135(145) μm long, bifid to 0.4–0.5; lobes triangular, acute, 4–5 cells wide on sterile leaves (only sporadic leaves with lobes 6 cells wide), ending in a single cell or sporadically to commonly in a uniseriate row of 2 cells, the terminal cells not elongated or sporadically elongated and incurved but not otherwise differentiated; disc 4–5 cells high from sinus base to leaf base, with margins entire but isolated leaves with 1(2) weak lateral teeth formed by projecting ends of marginal cells. Cells firm-walled but with lumina ± angular, at lobe base 11–14 μm wide × 17–19 μm long, rather irregular in shape, the cells within the lobes mostly quadrate, the cells at leaf base appreciably larger. Oil-bodies (Schuster, 1996a) smooth to very obscurely granular, subhomogeneous (no evident internal structure), 3–6 per cell, tiny, much smaller than chloroplasts, 1–1.6 × 1.2–1.75 μm. Underleaves present throughout, usually lanceolate, suberect from a spreading base and often with apex incurved, less than 0.25× the leaf length, usually only 3–4(6) cells broad at base, the apices sometimes bidentate with strongly elongated cells forming the lobes. Asexual reproduction absent.

Dioecious (?sometimes pseudodioecious). ♂ and ♀ Gametangia on ± elongated, unspecialized axes. Androecia soon becoming intercalary, brownish, at times with faint reddish pigmentation, usually exceedingly compact, only 230–250(300) μm broad and developed on weak and very slender shoots, usually only (160)200–250 μm broad, with exceedingly remote leaves; bracts in 3–5 pairs, very closely imbricate, mutually ensheathing, concave, only moderately ventricose, equally bifid, the lobes triangular, often strongly incurved, often ending in a uniseriate row of 2 elongated cells, the lobe margins entire to, at most, with 1(2) obscure teeth. Gynoecia, if unfertilized, always innovating, the innovations again soon fertile, the gynoecia on elongated shoots that are more vigorous than the ♂ shoots (to 350–385 μm wide), with leaves less remote and lobes sometimes 6–7 cells wide, the apices acute, often strongly incurved. ♀ Bracts (unfertilized gynoecia) connate with one another, the bracteole connate on one side for 0.25–0.35 and more shallowly so on the other side, the bracts and bracteole forming an erect sheath clearly investing the perianth; bracts broadly quadrate or rounded-quadrate, the bracteole oblong to oblong-ovate, ca. 270 μm wide × 400 μm long, usually bifid to 0.3–0.4 bifid, the lobes of bracts and bracteole irregularly denticulate. Perianth mouth of hyaline cells in 2–3 tiers, strongly elongated, the terminal cells 7–10 μm wide basally × 38–54 μm long (4.5–6[8]:1), thick-walled, especially at the tapered and free tips, but lumina distinct; cells below the hyaline apex becoming oblong to oblong-quadrate, less thick-walled.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: North Island (700 m).

Known from two collections from the type locality. The Otupaka "Frost Flats" is an open, low-lying area with rather dense scrub of *Leptospermum scoparium* and *Dracophyllum subulatum* with abundant *Cladonia*, and is a rigorous habitat for liverworts. At this site desiccation occurs regularly, and plants are subjected to strong frosts and hardly shaded by the low (0.5–1 m tall) shrubs of *L. scoparium* and *Dracophyllum*. *Lophozia pumicicola* also occurred at the site.

Comments: *Cephaloziella invisa* is distinct in having rather shallowly bilobed, entire-margined leaves, which when flattened have a rounded and wide sinus, which is unusual for the genus. The disc is usually only 4–5 cells high from leaf base to the sinus base. The leaf lobes are usually 4–5 cells wide at the base and terminate in a triangular cell or a uniseriate

row of 2 subisodiametric cells. Plants are dioecious, with ♂ and ♀ gametangia on long, unspecialized axes, do not produce gemmae and are green (but brown in lower, buried sectors), but may develop very local deep purplish pigmentation. The androecia are often distinctly compact and the bracts have entire lobes. The ♀ bract lobes are long-acute to subacuminate and characteristically hooked at the attenuated tip, and the perianth mouth has notably elongated cells, often 4–6:1 or longer.

Cephaloziella grandiretis (R.M.Schust.) R.M.Schust.

Cephaloziella byssacea subsp. *grandiretis* R.M.Schust., Nova Hedwigia 22: 195. *pl. 18: 10–17.* 1972 (1971). *Cephaloziella grandiretis* (R.M.Schust.) R.M.Schust., Nova Hedwigia 63: 35. 1996. Holotype: New Zealand, South Is., Fiordland Natl. Park, Humboldt Mtns., track from Lake MacKenzie to Harris Saddle, ca. 4000 ft., *Schuster 67-356.*

Plants anisophyllous, vigorous, helophytic, soft-textured, clear green to locally vinaceous or brownish purple (at least in upper portions of leaves), creeping to loosely caespitose, to 350–400 μm wide with leaves. Branching remote and irregular, the branches all ventral-intercalary; stolons or flagelliform branches absent. Stems stout, flexuous, the cortical cells weakly thick-walled, without cellular projections but with weak striolations. Leaves variable, erect or suberect to occasionally obliquely spreading, usually loosely folded-conduplicate, exceptionally remote, transverse to perceptibly succubous in insertion but transversely oriented and ± vertical, usually short-oblong or subquadrate to ovate-oblong, large, 300–380(410) μm wide × 350–410(515) μm long, bilobed to (0.65)0.7–0.8; lobes lanceolate-triangular, 8–11(14) cells broad at base, apices often incurved, ending in a sharp tip formed of 1–2(3) rather elongated cells; margins often crenulate-dentate to sparsely denticulate, but disc margins often with 1–2 coarse basal teeth or laciniae or accessory lobes; abaxial face of leaf smooth, or occasionally armed with low, gibbous, 1–2(3)-celled projections, but never armed with spinose processes; sinus with the V-shaped base sometimes reflexed. Cells thin-walled or the walls feebly thickened, large, at lobe bases 15–19(21) μm wide × (18)20–26(30) μm long; surface with low, rather coarse and closely set papillae. Oil-bodies (Schuster, 1972a) (3–5)6–12(15) per cell, ellipsoidal and 2.8–3.2 × 4–4.5 μm to 4 × 5.2 μm, or spherical and 2–4.2 μm in diam. Underleaves present throughout, very variable, large, oblong to irregularly quadrate, bifid or toothed or both, or with 1–several basal teeth or laciniae; abaxial faces smooth. Gemmae lacking (type) or present.

Dioecious. Androecia becoming intercalary; ♂ Bracts in 3–6 imbricate pairs. Gynoecia not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1220 m).

Known only from the type, collected in the penalpine tussock zone on peaty ground at the edge of a tarn, mixed with *Hygrolembidium acrocladum.*

Comments: This species is similar to *Cephaloziella byssacea* in 1) the remote leaves, which tend to have suberect lobes from a somewhat spreading base; 2) large and conspicuous underleaves throughout; 3) leaf lobes mostly 9–10 or more cells broad at the base (although the lobes may be up to 14 cells wide in larger leaves); 4) development of intensely violet or purplish pigmentation; and 5) a tendency, on some shoots, for development of abaxial cellular projections of the basal part of the leaf disc. In fact, *C. grandiretis* was originally regarded as a subspecies of *C. byssacea* by Schuster (1972a).

Cephaloziella grandiretis differs from *C. byssacea* in 1) the much larger leaf cells, which are the largest known for any of our *Cephaloziella* species, 15–19(21) μm wide × (18)20–26(30) μm long at lobe bases vs. (8)9–12(13) μm wide × 12–15 μm long in *C. byssacea*; 2) the more deeply divided leaves, bifid to 0.7–0.8 vs. to 0.5–0.65 in *C. byssacea*; and 3) the more numerous oil-bodies per cell, usually 6–12 per cell vs. 2–3(5) per cell in *C. byssacea*.

Cephaloziella nothogena R.M.Schust.

Cephaloziella nothogena R.M.Schust., Nova Hedwigia 63: 37. *f. 8.* 1996. Holotype: New Zealand, North Is., Tongariro Natl. Park, open valley at head of Mangatepopo Stream, *Schuster 95-1371*.

Plants usually gregarious in small, dense, interwoven patches, mostly amidst mosses, occasionally scattered, green (when shaded) to brownish, the perianths and bracts locally reddish pigmented, the sterile ones 190–225 μm wide, only 3–6 mm high. Branching common, irregular, the branches all intercalary, all or at least predominately ventral-intercalary, never strongly elongating (the plants forming a low turf under optimal conditions). Stem with cortical cells firm-walled. Rhizoids colorless, abundantly produced. Leaves rather stiff, obliquely spreading, *in situ* very weakly folded below the sinus, which is sometimes feebly gibbous or recurved, transversely inserted dorsally but somewhat obliquely ventrally, unistratose, rounded-quadrate in outline (when flattened), varying from 150 μm wide × 160 μm long to 185–200 μm wide × 190–215 μm long, toward shoot apices to 210 μm wide × 170–190 μm long, bilobed to (0.35)0.4–0.55; lobes mostly blunt or narrowly rounded at the tips (acute on leaves of weak shoots), 8–9 cells broad at the base; leaf margins smooth, entire; abaxial face unarmed; sinus subacute to somewhat obtuse on flattened leaves, the sinus base blunt or rounded. Cells of mature leaves usually pale to conspicuously brownish pigmented, with walls weakly thickened, the angles rounded, at lobe bases 11–15 × 13–18 μm up to (11)13–17 μm wide × 21–28 μm long; surface very finely verrucose, toward leaf bases becoming striolate. Underleaves present throughout on mature sterile axes, spreading and visible in lateral aspect of plant, mostly lingulate or ovate-lingulate, typically at least 0.15–0.2 the area of leaves on vigorous shoots; apex usually rounded-truncate and retuse or sometimes shallowly bilobed; underleaves on gemmiparous shoots becoming larger, often 0.5–0.6 as long and 0.25–0.3 the area of lateral leaves. Gemmae rare and sparingly produced, 2-celled, ellipsoid, smooth, the mature ones weakly rust-red, ca. 10–12 × 14–16 μm or smaller.

Paroecious and abundantly fertile; separate androecia not produced. Fertile shoot apices gradually larger-leaved, the 1–2 gyres of leaves below the ♀ bracts androecial, much larger, concave, with erect and sheathing lobes, the ♂ bracts subquadrate and rounded, bilobed to ca. 0.5; bract lobes triangular, those of inner bracts serrulate-denticulate like those of ♀ bracts, usually hyaline-margined for 1(2) rows; distal-most gyre of ♂ bracts accompanied by a large, usually bifid bracteole; antheridia 1 per bract, the stalk only 4–5 cells long, uniseriate. Gynoecia with bracts variable: mostly in 2 series, rounded-quadrate, at times broadly so, bilobed to ca. 0.3–0.4, with sharply serrulate-denticulate margins and a sharp apex, sometimes one bract trilobed, then one lobe often crenulate-denticulate like perianth mouth, the bract then broader; bracteole connate with bract on one side for at least 0.25–0.3 its length, nearly free or weakly connate on the other side, large, usually broadly ovate, bifid to ca. 0.3–0.35, the lobes armed like those of bracts. Perianths closely sheathed at base by the ± appressed bracts, crowded, prominent, large for plant size, 290–350(400) μm wide × 740–950 μm long or more, green below, reddish to brownish red in median sectors, becoming prominently bleached

in distal third, deeply 4-plicate, the mouth narrowed but rather wide and open, truncate, crenulate-denticulate with the free tips of the thick-walled marginal cells, the marginal cells mostly 25–36(38) × 7–11 μm (ca. 3–5:1), isolated cells shorter and broad; perianth unistratose throughout.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: North Island (ca. 1200 m).

Known only from the type collection, on water-deposited, silty soil; the species grows under "difficult" conditions, on open ground, between mosses and in tiny gregarious patches, fully exposed to the sun, where desiccated for much of the time (Schuster, 1996a).

Comments: This is the only paroecious species of *Cephaloziella* in New Zealand. Perianths are copiously developed, prominent and subtended by ♀ bracts with serrulate-denticulate lobes, and directly below those bracts, 1–2 pairs of large, imbricate, concave leaves that bear antheridia in their axils. The perianth mouth is narrowed and truncate, but rather wide and open, and is crenulate-denticulate, with narrow, thick-walled marginal cells that are ca. 3–5:1. Underleaves are present throughout on mature sterile axes and are visible when shoots are examined in lateral aspect. Leaf lobes are often blunt or narrowly rounded at the apex (except acute on weak shoots) and 8–9 cells wide at the base, and the cells are relatively large, 11–15 × 13–18 μm up to (11)13–17 μm wide × 21–28 μm long at lobe bases. The species belongs to sect. *Rubellae* (see Schuster, 1980b, p. 112).

Cephaloziella exiliflora (Taylor) Douin

Jungermannia divaricata var. *exiliflora* Taylor *ex* Gottsche, Lindenb. & Nees, Syn. Hepat. 136. 1844. *Jungermannia exiliflora* (Taylor *ex* Gottsche, Lindenb. & Nees) Taylor, London J. Bot. 5: 279. 1846. *Cephalozia exiliflora* (Taylor *ex* Gottsche, Lindenb. & Nees) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 417. 1877. *Cephaloziella exiliflora* (Taylor *ex* Gottsche, Lindenb. & Nees) Douin, Mém. Soc. Bot. France 29: 72. 1920. Type: Australia, Swan River, *Drummond 295*.

Plants pulvinate and caespitose, typically forming pure, sometimes extensive patches on charred wood, copiously branched in the basal, whitish to bleached, small-leaved (but not microphyllous) shoot system, from which countless erect, usually unramified axes arise, only 4–5 mm high; distal portions of plants rust-red to reddish brown to, occasionally, purplish brown, but perianths bleached at least distally and peripheral parts of ♀ bracts sometimes decolorate. Leafy shoots minute, gradually larger-leaved, the basal decolorate sectors only 150–175 μm wide with leaves, gradually larger above and peripheral to gametangial regions, becoming 350–400 μm wide. Stems lacking pigments, the cortex hyaline, in one layer of weakly defined, moderately thick-walled cells not larger than medullary cells; medullary cells a little thinner walled, variable in size; mycorrhizal infection of cortex or medulla lacking. Leaves laterally spreading to erect-spreading, remote, concave to loosely folded, the mature ones of sterile portions of shoot sectors from 140–150 μm wide × long to 170 μm wide × 150 μm long, when flattened subquadrate to subquadrate-obtrapezoidal, only slightly wider toward apex than medially, bilobed to 0.5–0.6; lobes weakly to moderately divergent, the flanks usually weakly arched; lobes (4)6–7 cells broad usually (near gynoecia to 9–12 cells broad), the apices usually blunt (ending in 1 non-elongated cell or often 2 laterally juxtaposed cells), the lobes usually not incurved; sinus (on flattened leaves) obtuse (sometimes broadly so), with rounded sinus base. Cells firm-walled, variable: in distal, pigmented sectors the primary walls and

weak trigones hyaline, only the secondary wall layer adjoining lumen strongly brownish pigmented; in lower shoot sectors all leaf cells hyaline-walled; cells at lobe bases 10–14 μm wide × 13–18 μm long; surface smooth or (?) very obscurely papillose with low, ill-defined papillae locally. Underleaves on weak sterile shoot sectors very small but distinct, on vigorous shoot sectors lamelliform, often broadly triangular to quadrate, 45–55 μm wide × 50–65 μm long, larger toward gynoecia (and there usually bilobed). Gemmae lacking.

Pseudodioecious: ♂ and ♀ gametangia usually terminal on long, leafy axes, the ♀ often abundant and ♂ rare (then seemingly dioecious); connections between ♂ and ♀ gametangia often difficult to demonstrate. Androecia terminal (?always), compactly spicate and rather long, sometimes narrower distally; bracts in 6–10 pairs, closely imbricate, moderately ventricose, bilobed to ca. 0.45–0.55, the lobe margins entire, often blunt to narrowly rounded at the tips; pouched basal sector of bracts formed of relatively large, thinner-walled, elongated cells. Gynoecia terminal, apparently without innovations even in absence of fertilization, initially capitate, strongly pigmented (at most with very tips of bracts and subgynoecial leaves becoming hyaline), the 2–3(4) gyres of rather suddenly much larger and denser leaves concave, superficially mimicking a paroecious inflorescence; bracts of innermost series closely sheathing perianth, bilobed to ca. 0.4, the lobes triangular, mostly irregularly, sparingly denticulate to serrulate, the apex acute and usually ending in a single cell; bracteole connate for 0.35–0.5(0.6) its length with bract on one side or connate on both sides and then forming a conspicuously plicate sheath, the bracteole usually oblong, bifid to ca. 0.4–0.45, the lobes acute, paucidentate. Perianth usually decolorate to greenish throughout (mouth always bleached), 4–5-plicate in upper half, the weakly contracted mouth crenulate with thick-walled, elongated (usually 2.5–3.6:1) cells that are free only at the tips; perianth unistratose at least to near base. Sporophytes unknown.

Distribution and Ecology: New Zealand and Australia.

"A tiny plant, forming pure and sometimes extensive mats on charred wood, coming in as a pioneer after fires. *Cephaloziella exiliflora* is one of very few Austral Cephaloziellaceae that forms pure mats, rather than occurring as solitary or somewhat gregarious colonies. It forms almost a 'lawn' on burned logs: the countless shoots erect, closely caespitose, and copiously branched below..." (Schuster, 1996a, p. 43).

Comments: Separable from our other taxa of *Cephaloziella* by the following. 1) The proclivity for formation of pure patches on charred wood. 2) The pale or whitish, translucent older sectors of the caespitose colonies, with only the shoot tips being intensely reddish brown or purplish brown. 3) The tendency for ♀ branches to have blunt leaf lobe tips. 4) Gynoecia, even when not fertilized, do not produce subfloral innovations. 5) Androecia form terminal spikes that do not proliferate vegetatively distally, thus not becoming intercalary. 6) ♂ Bracts have lobe apices blunt to narrowly rounded and margins that are entire. 7) The dorsal margins of leaves on ♀ shoots, and often to a lesser extent ♂ shoots, are oriented edge-on or even weakly reflexed. 8) The leaves of vigorous shoots tend to be slightly folded in the region of the sinus. 9) The irregularly bilobed or often 3–5-lobulate ♀ bracteole apex in gyres of bracts + bracteoles just below the innermost cycle. Such lobulate bracteoles are unknown in other *Cephaloziella* species (Schuster, 1996a).

Schuster (1972a, 1980b) and Douin (1920) stated that the type of *Cephaloziella exiliflora* is clearly autoecious to paroecious, and Schuster (1996a, p. 45), after a study of the sexuality of the species, concluded "that some plants are clearly only gynoecial, yet a small minority are demonstrably autoecious."

Schuster (1996a) commented that the reproductive biology of this species should be studied, and remarked that some populations may be only gynoecial, whereas others may be nearly exclusively so. Schuster (1996a, p. 45) noted that in "some *Lejeunea* species, there may be 15–30 (or more) gynoecia for every androecium." It should be emphasized that the physical connection confirming the autoecious condition is often difficult to demonstrate and careful dissection of many plants is normally required.

Cephaloziella crassigyna (R.M.Schust.) R.M.Schust.

Cephaloziella aterrima var. *crassigyna* R.M.Schust., Nova Hedwigia 22: 211. *pl. 24, 25*. 1972 (1971). *Cephaloziella crassigyna* (R.M.Schust.) R.M.Schust., Nova Hedwigia 61: 556. 1995. Holotype: New Zealand, South Is., Fiordland Natl. Park, Humboldt Mtns., track from Lake Howden to Earland Falls, *Schuster 48697*.

Plants vigorous, intensely blackish to piceous but without trace of reddish pigments even on ♀ bracts and perianths, the semi-buried lower regions olive-green, the shoots (except on remote-leaved lower sectors) to 500 μm wide with leaves. Stems slender, smooth. Leaves mostly erect-spreading, remote, becoming contiguous only near gynoecia and in androecial sectors, never sheathing stem, loosely concave but never conduplicate-folded (except perhaps near gynoecia), oblong-ovate or short-oblong to subquadrate, mostly somewhat longer than broad, on gynoecial axes to 150–165 μm wide × 190–210 μm long, to 180–190 μm wide × 210–240 μm long, on lower, remote-leaved sectors of stems considerably smaller, entire and smooth-margined, bifid to 0.5–0.6; lobes equal or subequal, plane and not adaxially concave, becoming erect and with lobe apices often weakly incurved, entire, 8–13 cells wide on larger leaves, acute but usually ending in a single, non-differentiated cell; sinus V-shaped, not gibbous at base; disc 6–8 cells high, ca. 16 cells broad, the abaxial surface smooth, unarmed. Cells 9–12 μm wide × (12)13–16 μm long at lobe bases; surface with low, rather close and coarse cuticular papillae. Underleaves lacking or reduced to a mucilage papilla. Asexual reproduction (gemmae) lacking.

Autoecious but often pseudodioecious, the ♂ and ♀ branches long, often remote from each other. Androecia on long axes and/or innovations from unfertilized gynoecia, terminal but becoming intercalary, laxly spicate, not broader than adjacent vegetative areas; bracts in 3–5 or more pairs, pouched at base, the lobes erect, entire-margined. Gynoecia, if unfertilized, with 1–3 sometimes clustered innovations, the innovations elongating but sooner or later producing androecia or other gynoecia; bracts broadly rounded-quadrate, bilobed to 0.5, bluntly pointed at the apex, entire-margined but sinuous or weakly to obscurely 1–2-dentate with low, broad teeth, the sinus broadly V-shaped; bracteole connate to ca. 0.35–0.45 with bracts on both sides, usually ovate-lanceolate, the triangular apex normally unlobed and entire, mostly blunt to subacute. Perianth extremely long and slender at maturity, subterete below, deeply 4–5-plicate in distal half or more, only weakly and gently narrowed to the wide mouth; mouth crenulate from the free, thick-walled ends of weakly elongated (1.5–2.5:1) cells; perianth 4–5-stratose in basal 0.2–0.25, becoming 1–2-stratose in the middle and 1-stratose only above the middle. Calyptra thin, unistratose to near base.

Seta with 4 rows of very large inflated outer cells and 4 rows of tiny inner cells opposed to the outer ones.

Distribution and Ecology: Endemic to New Zealand: South Island (Humboldt Mtns., Westland EP). Known only from the type, which occurred in large patches on thin peaty soil over rather permanently moist, strongly insolated rock ledges, in the uppermost *Nothofagus menziesii* forest zone.

Comments: The perianth bases in this species are rigid, fleshy and 4–5-stratose in the basal 0.2–0.25. This feature is unknown in any other species of *Cephaloziella*, and at once will separate *C. crassigyna* (when perianths are present) from all other New Zealand species of the genus.

Confusion with *Cephalomitrion aterrimum* is possible. Both plants tend to form wiry, blackish shoots, and according to Schuster (2002a), tend to occur in alpine sites on seepage-wet rocks (although the type of *Cephaloziella crassigyna* is from the uppermost *Nothofagus menziesii* zone). *Cephaloziella crassigyna* has obliquely erect-spreading leaves that are clearly distinct from the stem, a strongly elongated perianth that is 4–5-stratose toward the base, and has fuscous pigmentation. *Cephalomitrion aterrimum*, on the other hand, has scale-like leaves that are closely appressed to the stem, so much so that the leaves are difficult to distinguish, short perianths that are unistratose or at most 2-stratose at the base, and develops vinaceous pigmentation.

Cephaloziella densifolia R.M.Schust.

Cephaloziella densifolia R.M.Schust., Nova Hedwigia 22: 199. *f. 19*. 1972 (1971). Holotype: New Zealand, Stewart Is., summit of Tin Ra., ca. 1200 ft., *Schuster 53011a*.

Plants compact, slenderly julaceous-clavate, green, the leaf lobes occasionally to frequently fuscous-tinged, the plants vigorous, the shoots 300–350 μm wide. Branching common, the branches intercalary, ventral and, occasionally, lateral; stolons occasional, long, leafless, originating from ventral surface of base of ventral leafy branches. Stems green, firm, the cortical cells thick-walled and guttulate, the lumina elliptical, the stems ± papillose in surface view. Leaves stiff in appearance, vertical, with base stiffly, obliquely spreading and with lobes suberect to erect, unusually densely imbricate, rarely contiguous, obtusely folded toward each other, transverse, subquadrate, 220–280 μm wide × 220–245 μm long, deeply bifid, to 0.7–0.8; lobes with margins often narrowly recurved (the lobes then characteristically abaxially concave and the leaf somewhat fluted in appearance), the lobes slightly unequal (the ventral larger), narrowly ovate-triangular to broadly lanceolate, sharp, usually 10–12 cells wide at base; keel very short; leaf margins consistently entire, even on subgynoecial leaves; sinus acute, the sinus base often recurved; abaxial face of leaf consistently without cellular projections. Cells tending to become guttulate, with thick walls, the middle lamella distinct, the cells at lobe bases ca. 9.5–11.5 μm wide × 12–16(17–19) μm long; surface with strong, close papillae. Oil-bodies (Schuster, 1972a) 2–3(4) per cell, colorless, subhomogeneous to faintly papillose-botryoidal, smooth and glistening, small, 3–3.3 μm in diam. and spherical, to ovoid and 2.8–3 × 3.5–4 μm, a few to 3.5–4.4 × 4–4.5 μm; oil-bodies often largely lacking in mature leaves; chloroplasts subequal to oil-bodies in size. Underleaves lacking (even on the most vigorous plants) or sporadically present as 1-celled spurs. Gemmae lacking.

Evidently autoecious. Androecia intercalary on main stems, compactly spicate; bracts closely imbricate, moderately ventricose at base, with entire margins, the lobes broad. Gynoecia on long branches or ± abbreviated ventral branches; bracts closely sheathing except

for lobe apices, connate with each other, like leaves except somewhat larger, with subentire to weakly crenulate-serrulate margins, the lobes triangular, acute, with inner margins and sinuses recurved (as on uppermost leaves); bracteole conspicuously connate. Perianth decolorate throughout, sharply 4–5-plicate for at least two thirds its length, slenderly oblong-obclavate, unistratose to base, the mouth moderately contracted; mouth shallowly plurilobulate and setulose-ciliolate with long, 1–2-celled teeth, the terminal cells tapered, 28–36 × 7–9 μm, the lower flanks of mouth crenulate by free ends of cells.

Sporophyte unknown.

Comments: Plants of this species differ from typical members of the genus in being much denser-leaved and more vigorous. Diagnostic are the rigid leaves with suberect to erect lobes, with the leaf loosely folded along the midline and delimiting only a very short keel. In fact, plants have the superficial aspect of a minute *Gymnomitrion cuspidatum* or of a small, green *Anthelia* (Schuster, 1972a). Distinctive also are the deeply bifid (to 0.7–0.8) leaves, which often have narrowly recurved lobe margins often lending the lobes characteristically abaxially concave. The leaf surface has strong close papillae. The perianth is unique among Austral members of *Cephaloziella* in the shallowly plurilobulate and setulose-ciliolate mouth, with long 1–2-celled teeth with the terminal cell tapered.

The species has been subdivided into two varieties, as follows.

Key to Varieties

1a. Cells with close, strong cuticular papillae; leaves with lobes 10–12 cells broad; freely branched . . . . . var. *densifolia* (p. 599)

1b. Cells smooth; leaves with lobes (5)6–9 cells broad; subsimple or rarely branched . . . . . var. *dubia* (p. 599)

Cephaloziella densifolia R.M.Schust. var. ***densifolia***

Plants with branching common; leaves with lobes 10–12 cells broad, the cells of leaves with close, strong cuticular papillae.

Distribution and Ecology: Endemic to New Zealand: Stewart Island (ca. 365 m). The type occurred admixed with *Kurzia compacta* and *Allisoniella scottii* over intermittently moist rocks in sun.

Cephaloziella densifolia var. ***dubia*** R.M.Schust.

Cephaloziella densifolia var. *dubia* R.M.Schust., Nova Hedwigia 22: 202. *f. 24: 1–9*. 1972 (1971). Holotype: New Zealand, North Is., E side of Coromandel Ra., along road from Whitianga to Coromandel, ca. 1000 ft., *Schuster 67-1700a*.

Plants with branching rare; leaves with lobes (5)6–9 cells broad, the cells of leaves smooth.

Distribution and Ecology: Endemic to New Zealand: North Island (305 m). Known only from the type, on friable sandstone walls admixed with *Jackiella curvata*.

Cephaloziella pseudocrassigyna R.M.Schust. *ex* J.J.Engel

[Fig. 128: 4, oil-bodies, p. 558]

Cephaloziella pseudocrassigyna R.M.Schust., Nova Hedwigia 63: 48. *f. 1: 12–14*. 1996, *nom. inval*. herbarium not specified. *Cephaloziella pseudocrassigyna* R.M.Schust. *ex* J.J.Engel, Novon 17: 313. 2007. Holotype: New Zealand, South Is., Fiordland Natl. Park, Mt. Burns, *Schuster 84-115*.

Plants soft-textured, light clear translucent green, exposed sectors rusty red. Stem unarmed. Leaves remote to contiguous, never folded or conduplicate, symmetrically bilobed, the lobes equal, usually 7–11 cells broad at base, blunt to subacute, entire, the abaxial face of leaves unarmed. Cells somewhat firm-walled, the lumina angular, the cells subisodiametric, ca. 11–13 μm wide × 11–15 μm long at lobe bases. Oil-bodies (Schuster, 1996a) usually 2–3 per cell, faintly granular, almost smooth, rather large, 3–4.5 μm and spherical to ovoid and 4 × 4.5–5.5 μm to 3.5 × 4.8 μm, rarely isolated ones only 2.5 μm in diam. Underleaves (sterile shoots) lacking. Gemmae unknown.

Autoecious, but pseudodioecious. Perianth with 5 blunt to rounded plicae, the mouth setulose with cells strongly elongated, usually 4–5.5:1, free at their tapered, narrow, thick-walled apices; perianth 1-stratose at base.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (930 m). Type material was found on peaty ground of a small rill in a late snow area. The only other known collection is from an exposed thick peaty soil layer over rock in a boggy area within a mosaic of wet depressions, tussock grass, *Dracophyllum*, *Libocedrus bidwillii* and small thickets of *Nothofagus solandri* var. *cliffortioides* (Bealey Valley track, Arthur's Pass Natl. Park, Canterbury, 930 m).

Comments: Plants are rather vigorous for the genus and in the field appear somewhat like a miniature *Allisoniella*. Leaves are concave, often contiguous, with lobes suberect, often blunt to subacute and 7–11 cells broad at base. Cells are firm-walled, but the lumina are angular and never guttulate. Perianths are unistratose, bluntly 5-plicate and the mouth is setulose, with free ends of the cells at the mouth narrow (4–5.5:1), tapered and thick-walled.

The oil-bodies of the Bealey Valley track plant (Fig. 128: 4, *leg. Engel* and *von Konrat*) are small and inconspicuous, dull, opaque, 2–4 per cell in lower to middle lobe cells, and irregularly roughened with a faintly lumpy aspect, the oil-bodies each differing in their irregularity.

Cephaloziella varians (Gottsche) Steph.

Jungermannia varians Gottsche, Ergebn. Deutsch. Polar-Exped. 2(16): 452. *pl. 7, f. 1, 2*. 1890. *Cephalozia varians* (Gottsche) Steph., Résult. Voy. S. Y. Belgica 1897–1899, 6(5): 5. 1901. *Cephaloziella varians* (Gottsche) Steph., Wiss. Ergebn. Schwed. Südpolar-Exped. 1901–1903, 4(1): 4. 1905. *Lepidoziella varians* (Gottsche) Mahu, Bol. Antárt. Chileno 7: 3. 1987, *nom. inval*. Type: South Georgia, Penguin Bay, *Will 35*.

Cephalozia divaricata var. *verrucosa* C.E.O.Jensen, Meddel. Gronland 15: 374. 1898 (1897). *Cephalozia verrucosa* (C.E.O.Jensen) Bryhn & Kaal. *in* Bryhn, Rep. Second Norweg. Arctic Exped. (2) 11: 45. 1906, *hom. illeg. non C. verrucosa* Steph., Hedwigia 32: 1893. *Cephaloziella verrucosa* (C. Jens.) Bryhn & Kaal. *in* Bryhn, Vidensk.-Selsk., Forh. Kristiania 1908 (5): 4. 1908. Type: Greenland, Scoresby Sound, *Hartz*.

Cephaloziella arctica Bryhn & Douin *in* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland, ed. 2, 6(2): 159. *f. 45*. 1913. Type: Canada, Ellesmere Is., *Simmons*.
Cephaloziella alpina Douin, Rev. Gén. Bot. 28: 269. 1916. Type: ?
Cephaloziella glacialis Douin, Soc. Bot. France, Mém. 29: 71. 1920. Type: Scandinavian Alps.
Cephaloziella antarctica Douin, Soc. Bot. France, Mém. 29: 78. 1920. Lectotype (*fide* Bednarek-Ochyra et al., 2000): "…Terres antarcticques Canal de la Belgique, sur les rochers isolées au milieu d'un glacier à som… Exp. ant. belg. 12 feb. 98."
Cephaloziella varians (Gottsche) Steph. fo. *minor* Grolle, Bull. Brit. Antarct. Surv. 28: 83. 1972, *nom. nud*. Type: South Sandwich Is., Candlemas Is., western end of eastern lagoon, *Longton 597*.

Plants delicate, creeping to suberect, brownish green to deep violet to purplish brown or purplish black, small, 180–300 μm wide, 2–5 mm long. Branching sparse, the branches normally exclusively lateral-intercalary. Stems rather rigid, the cortical cells ± thin- to strongly thick-walled and guttulate; medullary cells somewhat smaller. Rhizoids hyaline, rare or rather common. Leaves usually purplish or ± violet-brown, at least near tips, erect to suberect to obliquely spreading, distant to approximate, transverse to subtransversely inserted, weakly to moderately concave (often loosely sheathing stem), mostly 1.5–2× as wide as stem, subquadrate to short-oblong when flattened, 170–225 μm wide and long, bilobed to 0.5–0.7; lobes little divergent, narrowly ovate to ovate-triangular, erect and often ± incurved at tips, relatively broad, the base usually 6–9, occasionally 10–12(14), cells wide, terminating in 1(2) superposed cells, or blunt to ± rounded, the lobes entire; sinus sharp, never gibbous or reflexed at base. Cells with walls thin to ± strongly thick-walled, moderately small, usually 11–14 μm wide × 12–16 μm long; surface usually smooth (in pachydermous forms ± verruculose). Oil-bodies (Schuster, 1980b *sub Cephaloziella arctica*) 2–7 per cell, glistening and conspicuous, nearly homogeneous in appearance, 2–3.2 × 2.5–3.6 μm, ovoid to ellipsoid, averaging somewhat smaller than chloroplasts (which are 3.5–4 μm long). Underleaves usually present throughout on mature, robust shoots (on weak shoots often sparse and very small), small and lingulate to lanceolate or bilobed, 3–6 cells high × 2–4 cells wide, larger in androecia. Gemmae usually violet, 2-celled, smooth or with a weak projection at each end, ellipsoidal-fusiform, 10–12 × 18–22 μm.

Autoecious, usually fertile. Androecial branches usually numerous and conspicuous, often arising from beneath unfertilized ♀ inflorescences, at other times as ventral branches a short distance beneath apices of fertilized ♀ shoots; androecia terminal but becoming intercalary, compactly but narrowly spicate; bracts almost always deep violet or violet-black (even when rest of plant is only slightly pigmented), in 4–10 pairs, imbricate, erect, bilobed, with ± incurved lobe apices, usually entire-margined, ventricose at base; antheridia 1 per bract. Gynoecia almost always on ± elongate, leafy shoots, often with 1–several subinvolucral innovations (which are more often ♂ than ♀); bracts often vinaceous or purplish but with margins decolorate, ovate to subquadrate, bilobed to 0.45–0.6, the lobes broadly ovate-triangular to ovate, ca. 9–14 cells wide, nearly entire-margined or finely and remotely denticulate; bracteole usually considerably smaller than bracts, 2(or irregularly 3–several)-lobed, connate for 0.1–0.3 with bracts. Perianth oblong to oblong-clavate, the apical region, at least, formed of slightly to ± strongly thick-walled, rectangular cells, decolorate in apical 2–5 or more rows; mouth cells crenulate by cells that are laterally free only near the summit and thus ± weakly projecting, the cells ca. 12 μm wide × 18–24 μm long.

Capsule ovoid-ellipsoidal, the outer layer of wall with nodular thickenings; inner layer of cells with semiannular bands, the bands narrow.

Spores 9–12 μm in diam., delicately verruculose. Elaters 7–8 μm in diam., 2-spiral.

Distribution and Ecology: Bipolar, in the Northern Hemisphere probably pan-Holarctic, with a probable continuous distribution in the Arctic (often in basic-rich areas). Apparently very widespread and the most ubiquitous species of the genus in the Arctic; on the Arctic coast of Ellesmere Island it is one of the two commonest hepatics (Schuster, 1980b, p. 150) and it "is perhaps the commonest and most widespread *Cephaloziella* in Greenland and is one of the most abundant species of Hepaticae found there" (Schuster and Damsholt, 1974, p. 326). In the Antipodes in New Zealand, 1615 m on South Island, South Georgia (type of *Cephaloziella varians*) and in the Antarctic, where the species "is the commonest, most widespread and the most abundant species of liverwort in Antarctica. It is the only liverwort known to occur in the Continental Antarctic..." (Bednarek-Ochyra et al., 2000, p. 87).

In New Zealand the species is known only from near the summit of the "Old Man" (Old Man Ra., Otago), where it grew on peaty soil along a small alpine rill, with *Lophozia excisa*, *L. autoica*, *Cephalozia austrigena* and *Hygrolembidium acrocladum* (Schuster, 1972a).

Comments: Schuster (1980b) deals with this species in detail and provides numerous figures, and Schuster and Damsholt (1974) also provided a discussion. Bednarek-Ochyra et al. (2000) provided useful comments on this species. The species is known from New Zealand only from the following, which was described from a collection from the Old Man Ra.

Cephaloziella varians subsp. ***subantarctica*** (R.M.Schust.) R.M.Schust. *ex* J.J.Engel

Cephaloziella arctica subsp. *subantarctica* R.M.Schust., Nova Hedwigia 22: 197. *pl. 15*. 1972 (1971). *Cephaloziella varians* subsp. *subantarctica* (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, Novon 17: 314. 2007. Holotype: New Zealand, South Is., Otago Prov., Old Man Ra., near summit of the "Old Man," 5300 ft., *Schuster 67-515a*.

Distribution: New Zealand; Australia: Tasmania, Victoria, South Australia (Scott, 1985).

Comments: Schuster (1996a, p. 49) remarked that "the status of subsp. *subantarctica* needs re-newed investigation from more copious collections," and for that reason, and also since we did not examine the type of this taxon, a taxonomic disposition is not made here.

Schuster (1972a) remarked that plants of this subspecies have some characters that may offer confusion with *Cephaloziella byssacea*, e.g., the rather large underleaves, the mostly folded leaves, and the more weakly connate gynoecial bracts. Presence of an autoecious inflorescence will immediately distinguish *C. varians* from the dioecious *C. byssacea*.

Schuster (1972a, p. 197) commented that plants of *Cephaloziella arctica* subsp. *subantarctica* are "autoecious but usually pseudodioecious (♂ and ♀ branches are often separated through decay of older shoot sectors"). Here and elsewhere the presence of a pseudodioecious condition must be treated with care, especially in populations where androecia and gynoecia are both terminal and mostly on very long branches. At times ♂ and ♀ gametangia are so remote from each other that intervening shoot sectors are often dead or dying by the time antheridia and perianths form, so that confusion of sexuality is a possibility. Care and patience are required to dissect out whole plants that demonstrate connections between ♂ and ♀ gametangia.

Cephaloziella exigua R.M.Schust.

Cephaloziella exigua R.M.Schust., Nova Hedwigia 63: 49. *f. 11*. 1996. Holotype: New Zealand, South Is., Milford Sound, along trail from hotel to Bowen Falls, sea level, *Schuster 48602*.

Plants straggly, creeping as isolated, sinuous stems among *Herbertus*, lacking secondary pigmentation above or the leaves at shoot tips intensely vinaceous, the stems whitish above but with age weakly brownish, minute, the shoot with leaves little broader than stem alone, to, at most, 90–100 μm wide with leaves; shoot apices terete, the minute leaves distally overarching shoot apex, concave and erect-appressed like lower leaves. Branching sparing and irregular, the branches all intercalary, ventral and (?)lateral, widely spreading, almost immediately similar to parent axis in diameter. Stems rigid and rather wiry, whitish and translucent above, with age faintly brownish, the cortex in 1(2) layers of exceedingly thick-walled cells, the cortex in surface view with rounded to elliptical lumina only 3.4–7.5 μm wide × 12–18 μm long. Leaves erect-appressed, closely adnate to stem (the distal portions of lobes weakly erect-spreading, but the sharp lobe tips then again incurved), on older shoot sectors leaves hyaline and so closely applied to stem as to be almost imperceptible; leaves exceedingly remote, the spaces between leaves 3–6× as long as leaves, transverse, tending to be asymmetrical, with the ventral half somewhat ampliate, the leaves reniform to broadly quadrate-rounded in outline (but outline almost impossible to decipher, since the tiny leaves can hardly be dissected free), to 75–80 μm wide × 55–62(72) μm long, always a little to much wider than long, bilobed to ca. 0.5–0.6, the leaf margins serrulate with apices of projecting cells; lobes equal, sharply pointed, the prominent end cell with tip strongly thick-walled, often inserted on a strongly transverse to crescentic cell, the lobes (3)4(5) cells broad at base, the margins serrulate-crenulate with the thick-walled tips of conspicuously projecting cells; lamina 2–4 cells high from sinus base to leaf base, 8–9 cells wide. Cells of the ± hyaline shoot apices locally with intense vinaceous-pigmented walls, but in mature shoot sectors, the leaves decolorate and transparent; cells thick-walled, with maturity very thick-walled and with lumina rounded, becoming guttulate, at lobe bases from 8–11 × 10–14 μm, to locally, 10–12 × 12–19 μm; surface smooth. Underleaves reduced to a slime papilla or, occasionally, a stalked slime papilla, at most formed of 2 superposed cells. Gemmae lacking.

Otherwise unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (sea level). Known only from the type, which was found creeping between shoots of *Herbertus oldfieldianus* over seepage-wet rocks, and admixed with *Acromastigum brachyphyllum*, *Adelanthus occlusus*, *Anastrophyllum schismoides*, *Cheilolejeunea* spp., *Cryptochila pseudocclusa*, *Goebeliella cornigera*, *Lepicolea*, *Trichotemnoma corrugatum*, *Heteroscyphus* (= *Tetracymbaliella*) and other taxa.

Comments: Perhaps the smallest hepatic ever found, with leafy shoots only 90–100 μm in diam. and "far smaller than any other *Cephaloziella*" (Schuster, 1996a, p. 53). Shoots are thread-like, with very remote, closely appressed, scale-like, relatively few-celled leaves. The stem cortical cells in surface view are guttulate with exceedingly thick-walled cells with rounded lumina.

Subg. ***Evansia*** Müll.Frib.

Cephaloziella subg. *Evansia* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland, ed. 2, 6(2): 787. 1916. *Evansia* Douin & Schiffn. *in* Douin, Rev. Bryol. 40: 66. Sept.–Oct. 1913; Douin, Bull. Soc. Bot. France 60: 480, 492. 17 Jan. 1914 (1913), *non Evansia* Salisbury, Trans. Hort. Soc. London 1: 303. 1812 (*Iridaceae*). Type: *C. dentata* (Raddi) Migula.

Branching exclusively lateral- and ventral-intercalary. Leaves with lobes of all but the most juvenile leaves with sharply toothed margins. Underleaves distinct. Gemmae broadly ellipsoid to sporadically subquadrate, covered with rounded tubercles. Dioecious. Bracts and bracteole sharply acute at the apex, the margins strongly toothed.

Type: *Cephaloziella dentata* (Raddi) Müll.Frib. of Europe.

Evansia includes possibly only 2–3 species, one in New Zealand.

Cephaloziella subspinosa R.M.Schust.

Cephaloziella subspinosa R.M.Schust., Nova Hedwigia 22: 210. *pl. 24: 10–14*. 1972 (1971). Holotype: New Zealand, North Is., Mangamuka Reserve, SE of Kaitaia, ca. 1000 ft., *Schuster 67-1114a*.

Plants clear green, with bright brownish shoot apices on exposed shoot sectors, small, to 400–425 μm wide. Branching sparingly. Stem smooth. Leaves vertical, stiffly spreading, loosely folded or conduplicate, remote, transversely inserted, broadly subquadrate when flattened, 175–185(205) μm wide × 150(175) μm long, bifid to at most 0.65; lobes sharply triangular, straight, never incurved, 6–9 cells broad at base, terminating in a single, somewhat weakly elongated, typically tuberculate-tipped cell, the margins with scattered, sharp-tipped, 1-celled teeth whose tips are ± thick-walled; disc margins with a few teeth similar to those of the lobes, the teeth 11–14 per leaf (on weak plants the dentition lacking or vestigial but all mature plants with at least a few such sharp-tipped teeth), the abaxial surface of disc smooth and cells not tuberculate; sinus broadly U-shaped at base and strongly gibbose and recurved. Cells usually colorless, smooth, thick-walled, with a distinct middle lamella, strongly variable, from 10–13 × 10–14 μm at margins and apices to 16–18 × 20–26 μm at base, often with 2–3 much larger cells. Oil-bodies (Schuster, 1972a) not glistening, (1)2–3(4) in most cells, 2–4(5) in larger basal and sub-basal cells, lacking in many marginal and submarginal cells, obscurely papillose-botryoidal, subspherical, 2–3 × 3–4 μm. Underleaves well developed, polymorphic, either bifid with 2–3-celled lobes or unlobed and ending in a jagged tooth and with 2–4 supplementary teeth. Gemmae lacking (type) or present and 2-celled, subspherical, covered with rounded, thick-walled tubercles.

Dioecious. Only ♂ known.

Distribution and Ecology: Endemic to New Zealand: North Island (305–380 m). Known only from two stations: the type station, on a loamy clay bank, mixed with *Paracromastigum furcifolium*, *P. macrostipum* and *Isotachis* cf. *lyallii* under *Leptospermum scoparium* at the edge of a disused road (Schuster, 1972a). Also known from along a stream in Whirinaki (*leg. Schuster*), where growing as straggly stems mixed with small acrocarpous mosses and *Cephaloziella muelleriana*. In both cases on mineral soil.

Comments: The sharp but small teeth of the leaves of larger plants are diagnostic for the species. Such teeth are produced independently of gemma formation, unlike many other *Cephaloziella* species, which develop dentition of gemmiferous leaves.

Cephaloziella subspinosa is a member of subgenus *Evansia*, in which gemmae are covered with coarse rounded papillae. Our other *Cephaloziella* species have gemmae that are ovoid to ellipsoidal and smooth, often with a slight mamillate projection at the ends (citroniform), or gemmae are absent altogether (10 species).

The species is also notable in the marked size discrepancy between marginal cells and median/basal cells (see Schuster, 1996a, fig. 12: 4).

Schuster (1996a) commented that *Cephaloziella pellucida* of New Zealand, and *C. squarrosula* and *C. hirta* of Australia, may be extremes of a single species. This complex needs further study. For example, Douin (1920) states that *C. squarrosula* is paroecious, but Stephani (1898–1924 [1908]) says it is dioecious. *Cephaloziella hirta* is stated to be dioecious by Stephani (1898–1924 [1908]).

This species is one of a relatively few lowland taxa of North Island. The others are *Cephaloziella muelleriana* (Whirinaki River, 380 m), *C. invisa* (Otupaka Frost Flats, 700 m) and *C. densifolia* var. *dubia* (Coromandel Ra., 305 m). Most of our *Cephaloziella* taxa occur at upper elevations (often alpine zone) in the South Island.

Subg. ***Distichopsis*** R.M.Schust.

Cephaloziella subg. *Distichopsis* R.M.Schust., Nova Hedwigia 63: 56. 1996. Type: *C. pellucida* R.M.Schust.

Shoot apices strikingly complanate, with folded, rather dense leaves, with shoot tips upcurved. Leaves with bases sheathing, the leaves asymmetrical, with the ventral margin ampliate, the ampliate sector denticulate or crenulate-denticulate, in part or wholly by cells elongated at right or oblique angles to the leaf margin. Leaves with rather distinct median basal field of larger, conspicuously elongated cells.

Cephaloziella pellucida R.M.Schust.

Cephaloziella pellucida R.M.Schust., Nova Hedwigia 63: 57. *f. 13*. 1996. Holotype: New Zealand, South Is., Canterbury Prov., Arthur's Pass Natl. Park, Temple Basin, 4500–4800 ft., *Schuster 84-899*.

Plants erect, growing amidst mosses, straggly, when dry white and opaque, when moist translucent aside from the ± opaque medulla of the stem, only the uppermost leaves of complanate-leaved shoots locally pigmented brownish purple, the shoots very small (lower, terete or subterete leafy shoots only 130–185 μm wide, apical distichous-leaved sectors to 270–300(400) μm wide, strongly complanate, the shoot tips sharply upcurved), the sinuous shoots long and stringy, under 5–6 mm long but indeterminate in length. Branching very sparing and irregular, the branches all lateral-intercalary, soon equal in vigor to main axis. Stem wiry and rigid, the cortical cells unpigmented, hyaline, undifferentiated, of notably thick-walled cells, the cortical cells in surface view subquadrate to short-oblong, with strongly thickened longi-

tudinal and transverse walls, the surface striolate; medullary cells with pale yellowish or yellowish brown, very thick walls, the lumina guttulate, the cells averaging a little smaller than those of cortex. Rhizoids few, only on lower shoot sectors, scattered, short, hyaline, usually solitary. Leaves varying greatly in form, density and orientation: on lower shoot sectors sheathing in their basal 0.5–0.65, with ± spreading lobes, often with the spreading lobes conspicuously denticulate (at least on ventral margins and often on lobes); leaves on the remote- to contiguous-leaved sectors often smaller, 130–145 μm wide × 165–175 μm long, asymmetrically ovate, the dorsal half of leaf smaller and shorter, the dorsal margin straight or weakly arched; ventral half of leaf broader and longer, the ventral margin distinctly ampliate below and there conspicuously denticulate or crenulate with thick-walled cells, often elongated obliquely or at right angles to the margin; leaves asymmetrically bifid to 0.4–0.45, the lobes sharp, subentire to obscurely crenulate-denticulate with projecting or bowed-out free cell walls, the ventral lobe usually 4–5 cells broad, the dorsal lobe shorter, (3)4 cells broad. Leaves of upper sector of stem densely imbricate, the stem nearly or quite hidden in dorsal aspect, somewhat dorsally assurgent, complanate, sheathing only at the base and with the lobes widely spreading, the leaves more narrowly ovate, to 135 μm wide × 210–225 μm long, otherwise like the lower leaves, but denticulation of ventral margin often less pronounced. Cells everywhere thick-walled and lacking trigones, the lumina rather angular with rounded corners; cells in lobes tending to be inflated, the convexity often strongly thick-walled, sometimes lenticular (visible sometimes in cells of the ill-defined keel of complanate leaves); marginal cells in and near lobes 11–14 μm, measured tangentially; cells at lobe bases variable, 11–13 μm wide × 13–17 μm long to (ventral lobe) 13–17 μm wide × 13–18 μm long; cells in an ill-defined median basal field irregularly oblong, considerably larger and conspicuously elongated, the largest 11–17 × 21–30 μm; surface smooth. Underleaves lacking, not even slime papillae discernable, the ventral merophyte 1 cell broad. Asexual reproduction absent.

Androecia and gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (1370–1465 m). Known only from the type, among *Distichium capillaceum* in drip-wet crevices of cliff.

Comments: A distinctive plant with a number of features unique to the genus. 1) The shoot apices are complanate and artificially somewhat flattened and the tips are strongly upcurved, and in this distal sector the leaves are folded, densely imbricate and rather dorsally assurgent. This is the sector of the shoot that is exposed *in situ*, since only the distal portions of the plants are visible between the tufts of the moss *Distichium* (Schuster, 1996a). The lower sector of the shoot appears quite different: lower leaves ensheath the stem except for the narrowly acute lobes, which are stiffly obliquely spreading. 2) Leaves are asymmetrical, with the lower half of the ventral margin ampliate and denticulate or crenulate-denticulate by cells that are elongated at right or oblique angles to the leaf margin. 3) Plants have a peculiar bleached and translucent aspect, the leaves transparent and the cortical cells ± hyaline. Plants lack wall pigments except the spreading lobe tips of the uppermost leaves may have weakly warm brown or purplish brown pigmentation. 4) Leaves have a distinctive areolation, with presence of a median basal field of larger, conspicuously elongated cells. Schuster (1996a) remarked that species of *Cephaloziella* otherwise have basal cells that may be appreciably larger, but they never become conspicuously elongated and that mostly there is at best a slight increase in cell size from median to basal cells.

A more definitive taxonomic placement of this species must await discovery of gametangia.

Cephaloziella rufobrunnea R.M.Schust.

Cephaloziella rufobrunnea R.M.Schust., Beih. Nova Hedwigia 119: 144. *f. 265A*. 2002. Holotype: New Zealand, South Is., Fiordland, below Gertrude Cirque, NE of Homer Tunnel, 1740 m, *Schuster 95-2050a*.

Plants wiry, rusty red-brown, tiny, 165–265 μm wide. Branching sparing, the branches (only a few known) lateral-intercalary. Stems with cortex poorly differentiated, the cells (aside from free walls) leptodermous; medullary cells leptodermous. Leaves vertically oriented, often erect-spreading, somewhat distant to contiguous to weakly imbricate, often loosely folded, transverse, concave to canaliculate concave, broadly ovate to orbicular-ovate, 180–200 μm wide × long, bilobed to 0.2–0.3(0.35); lobes acute, triangular, the sinus V-shaped. Cells thin- to firm-walled, the angles of the lumina somewhat rounded, in median lamina 12–14 × 13–16(18) μm, in lobe middle 10–12 × 10–13 μm, to 12–14 × 13–18 μm basally; surface smooth or feebly striolate. Gemmae unknown.

?Dioecious, only putative ♂ known. Leaves in and near what appear to be androecia are denser, more concave and larger, but antheridia unknown. Androecia and gynoecia unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (1740 m).

Schuster (2002a, p. 144) remarked that "the type occurred amidst a fuscous, sterile, reduced *Jamesoniella*, with *Lophozia* cf. *bicrenata* (red gemmae), *Marsupella sprucei* and other taxa of 'difficult,' exposed sites."

Comments: Schuster (2002a) was uncertain of the affinities of the species and included it in the appendix to *Cephaloziella*. Plants have the appearance of a tiny *Anastrophyllum*, and the leaf shape and the shallow sinus immediately suggests lophozioids. On the other hand the thin-walled cells are much too small for an *Anastrophyllum* and more closely resemble those of a *Cephaloziella*.

The species is validly published in Schuster (2002a), though the essential elements are scattered—it has a Latin diagnosis, a type is cited in the figure legend (p. 145) and a herbarium is cited in the text (p. 144).

Family **ADELANTHACEAE** (Jörg.) Grolle

Adelanthaceae (Jörg.) Grolle, J. Hattori Bot. Lab. 35: 327. 1972. Tribe *Adelantheae* Jörg., Bergens Mus. Skr. 16: 257. 1934.

Plants strongly anisophyllous, firm to rather rigid, opaque or semiopaque, greenish, sometimes developing golden or brownish to fuscous (never reddish) pigments, medium to rather robust; leafy shoots ascending to erect and limited in height, usually unbranched except near base, arising from a system of creeping, rhizoidous, often interwoven, freely branched, leafless, whitish and colorless, plagiotropic and geotropic, stoloniform axes, the leafy shoots small-leaved below, often ± laterally compressed, often tapered and smaller-leaved distally, the shoot tips straight or often cernuous to circinate. Branching normally exclusively intercalary, ventral- or lateral-intercalary in origin, rarely (*Calyptrocolea*) with isolated *Frullania*-type branches, the branches usually from near bases of upright leafy shoots. Stems rigid, the cortex distinct, usually ± opaque, often with dark pigments, or (*Wettsteinia*) with a collapsing hyaloderm and firm-walled intracortical cells. Rhizoids at bases of erect leafy shoots but lack-

ing above, common and scattered on leafless horizontal axes. Leaves often subvertically oriented, often asymmetric, the insertion subtransverse to succubous, extending to stem midline dorsally, the leaves unlobed and entire, at times bidentate or bearing numerous, small, ± regular teeth, the dorsal margin never deflexed, usually decurrent. Cells with walls firm and equally thickened or thinner and with strong trigones, in some species clearly elongated at the median base and forming a ± well-defined vitta; surface smooth. Oil-bodies finely granular to botryoidal. Underleaves lacking or mere slime papillae or vestigial. Asexual reproduction lacking or by 1–2-celled, smooth, greenish gemmae.

Dioecious. ♂ and ♀ Branches reduced, highly abbreviated, determinate, ventral-intercalary, basitonic, originating only from stoloniform axes or the leafless basal portion of erect leafy axes. Androecia minute, spicate, often vermiform, frequently coiled, determinate in length, often whitish and translucent; bracts minute, imbricate, distinctly ventricose; antheridia 1(2) per bract, the stalk uniseriate; bracteoles few-celled, vestigial, lacking antheridia. Gynoecial branches lacking vegetative leaves; bracts in (1)2(3) series, relatively small, unlobed or 2(3)-lobed, with apices or margins often toothed; bracteoles similar or somewhat smaller. Perianth (when developed) trigonous, inflated, the mouth wide, lobulate-ciliate; perianth often reduced or lacking and then with elaboration of a fleshy, green, polystratose, cylindric-clavate shoot-calyptra.

Foot conoidal, without but more often with an elaborated haustorial collar. Seta massive, with 50–85 rows of outer rows surrounding numerous, internal cells that are ± similar or a little larger. Capsule short- to moderately long-ellipsoidal, the wall fleshy, 4–8-stratose; outer layer of cells often with imperfect two-phase ontogeny or (*Wettsteinia*) with cells mostly devoid of thickenings.

Spores granulate or with papillae and very short-vermiculate markings or baculate. Elaters 2–3-spiral.

Type: *Adelanthus* Mitt.

The *Adelanthaceae*, which occupy a very isolated position in the *Cephaloziineae*, are very largely Gondwanic in distribution and best developed in Australasia. The family consists of three genera; eight to nine are Neotropical-montane, two species occur in westernmost Europe, only one extends as far as Taiwan and no species occur in North America. All three genera occur in New Zealand. Most species of the family occur on soil or rocks, but a few (*Pseudomarsupidium* spp.) have become arboreal.

In *Adelanthus* and *Wettsteinia* all traces of a perianth have been lost and a fleshy shoot-calyptra is elaborated, bearing on its surface the unfertilized archegonia. A distinct perianth occurs only in *Pseudomarsupidium*. The species of *Pseudomarsupidium* are sometimes included in *Adelanthus*.

The generic name *Adelanthus* Mitt. (Mitten, 1864) is conserved against *Adelanthus* Endl., a flowering plant (see list of conserved names in Greuter et al., 2000), with *A. falcatus* (≡ *Jungermannia falcata* Hook.) listed as the conserved type. Schuster (1967b, 1967c, 2002a) has argued that the type of *Adelanthus* Mitt. should be *A. decipiens* (Hook.) Mitt. He includes *A. falcatus* in his own genus *Calyptrocolea* R.M.Schust., the holotype of which is *C. gemmipara* R.M.Schust. (Schuster, 1967c). However, since the type of *Adelanthus* Mitt. is conserved, a change in the listed type can only be brought about by conservation. According to Art. 14.8 (McNeil et al., 2006), "The listed type of a conserved name may not be changed except by the procedure outlined in Art. 14.12," i.e., by a formal proposal to the General

Committee to be published in *Taxon*. To date, such a proposal has not been made. For further discussion, see Grolle (1972a, 2003).

Pseudomarsupidium Herzog

Pseudomarsupidium Herzog, Svensk Bot. Tidskr. 47: 31. 1953.

Plants relatively soft-textured, dull green to brown to fuscous but never nitid, medium in size; leafy shoots stiffly ascending to erect, determinate, unbranched except toward their bases, arising from a system of creeping, rhizoidous, leafless, freely branched, stoloniform axes that typically form an intricate system of wiry, interwoven, root-like organs. Branches uniformly intercalary, predominantly ventral, sometimes lateral-intercalary and from near ventral bases of lower, reduced lateral leaves. Stems rigid, unpigmented or (*Pseudomarsupidium aureocinctum*) pigmented, with cortical cells persistent and not collapsing, in surface view usually short-rectangular, in cross section in 1(2) layers, rather ill-defined, weakly to moderately thick-walled (distinctly thickened in *P. aureocinctum*), a hyaloderm lacking. Leaves ± suberect to obliquely spreading, concave at least basally, asymmetric; apex undivided and entire or bidentate, the teeth short to long and spiniferous; margins entire, the dorsal margin often incurved, the base rather dilated, conspicuously long-decurrent, the ventral margin ± dilated. Cells with walls thin, with trigones distinct, nodose, at times confluent, the cells in median, distal and peripheral sectors isodiametric, the basal cells undifferentiated, not or hardly elongated, without differentiation of a vitta. Oil-bodies mostly 4–11 to 19 per cell, finely granular to coarsely papillose. Underleaves lacking. Asexual reproduction lacking (gemmae never developed).

♂ and ♀ Gametangia on strongly abbreviated intercalary branches lacking vegetative leaves, all or mostly from leafless lower sectors of plant or from stolons. Androecia minute, whitish, the bracts in (1)2–6 pairs small, imbricate, unlobed, ventricose. Gynoecia with 2–3(4) series of progressively larger bracts and bracteoles; innermost series of bracts largest, the apices variable, undivided and tapered to the summit or shallowly 2–3-lobulate and/or dentate to ciliate; bracteoles ± connate on 1 or both sides. Shoot-calyptra present, the wall usually 3–4(5)-layered. Perianth variable: large and then 3–5 times the length of bracts and then conspicuous, ovate to fusiform-elliptical, inflated, bluntly trigonous above, the mouth lobulate-ciliate, or abbreviated but distinct and inflated, or (sometimes in *Pseudomarsupidium piliferum*) vestigial, sometimes cut to the base into 3 bract-like segments with apices spinose-ciliate.

Capsule ellipsoidal, the wall (3)4–7-stratose; outer layer of with imperfect two-phase development, the longitudinal walls with strong nodule-like thickenings alternating with primary walls either devoid of thickenings or with a few nodular thickenings; innermost layer of cells with semiannular bands, the bands at times forked, at times anastomosing to delimit local fenestrae.

Spores tuberculate or baculate; spore:elater diam. ratio large, 2–4.1:1. Elaters bispiral.

Type: *Pseudomarsupidium piliferum* (Steph.) Herzog *ex* Grolle (≡ *Marsupidium piliferum* Steph.)

A genus interpreted here in the strict sense, with four species. *Pseudomarsupidium piliferum* is the only Austral species, occurring in New Zealand, Australia (Tasmania, Victoria, New South Wales), New Caledonia, southern South America, Juan Fernandez and Inaccessible Island. *Pseudomarsupidium decipiens* (Hook.) Grolle has a widespread distribution, being

broadly distributed in the Neotropics (Gradstein et al., 2001) including Brazil (Gradstein and Pinheiro da Costa, 2003), the Antilles, Great Britain, Ireland, NW France, Macronesia, South Africa and north in Africa to the Cameroons and Ethiopia. *Pseudomarsupidium crossii* (Spruce) J.J.Engel occurs in Colombia and Venezuela and *P. aureocinctum* (R.M.Schust.) J.J.Engel in Venezuela (see Engel, 2007).

References: Grolle (1972a, rev.; 2003); Schuster (1968b, 1969c, 2002a).

Pseudomarsupidium piliferum (Steph.) Herzog *ex* Grolle

[Plate 12C; Fig. 128: 5, oil-bodies, p. 558; Figs. 129, 130]

Marsupidium piliferum Steph., Sp. Hepat. 3: 386. 1908. *Pseudomarsupidium piliferum* (Steph.) Herzog *ex* Grolle, Trans. Brit. Bryol. Soc. 4: 443. 1963, *non Adelanthus piliferus* Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 184. 1934. Lectotype (*fide* Grolle, 1972a): Australia, New South Wales ("Australia felix"), *Ferd. von Müller* (G!); syntype: Chile, Corral, *Krause*, ex herb. Gottsche (G!).

Tylimanthus bisetulus Steph., Sp. Hepat. 6: 246. 1922. *Adelanthus bisetulus* (Steph.) Grolle, J. Hattori Bot. Lab. 35: 359. 1972. Lectotype (*fide* Grolle, 1972a): New Caledonia, in jugo Dogny, 1040 m, *Lerat 361* (G!).

Adelanthus humilis Steph., Sp. Hepat. 6: 446. 1924. Type: New Caledonia, in jugo Dogny, 1040 m, 1909, *Lerat 207* (G!).

Plants chestnut-brown, dull, the shoot system consisting of prostrate, copiously branched, basal stolons that are often partially embedded in the substrate, and erect, leafy shoots. Branching always ventral-intercalary, for the most part from basal sectors of plant, the stolons with small leaves with apices broadly rounded and devoid of spines and underleaves that are minute, inconspicuous and irregularly acute. Stems of erect shoots narrow for plant size, stiff and wiry, chestnut-brown; stem in cross section with cells ± uniform in size, the cortex in 1(2) layers, reddish brown, with thickened walls. Rhizoids copious, on all sides of stolons, lacking entirely from leafy sectors of erect branches. Leaves of erect shoots stiff, brittle, fragile, reduced and scale-like below, becoming densely imbricate, concave, not vittate, the orientation ± transverse to succubous, the insertion narrow, oblique and slightly recurved at ventral end, the leaves ovate to orbicular to feebly oblate, abruptly narrowed at the base; apex with 2(rarely 3), elongated, often ventrally bent or flexed, hyaline or pale brown awns (on suboptimal shoots reduced to thorns), the dorsal awn at juncture of apex and dorsal margin and typically appearing as a continuation of the margin, the awns consisting of a uniseriate row of to 9(10) cells, the awn cells elongated, 17–30 μm wide × (65)72–114 μm long (typically 2.4–6.6:1), with strongly thickened walls, the terminal cell sharply pointed, the apex and margins otherwise entire; dorsal margin often erect, inflexed and ± clasping the stem, particularly when dry, the base broadly decurrent by a distinct acute strip, ± straight to broadly and gently curved; ventral margin broadly ampliate. Cells with thin walls, with medium to weakly knot-like trigones; subapical cells isodiametric, 24–34 μm wide and long; median cells nearly isodiametric, 26–38 μm wide × 30–38 μm long; median-basal cells larger, not markedly elongated; marginal row of cells with exposed wall strongly thickened, the "half-trigones" along margin very large. Oil-bodies occupying a conspicuous portion of the cell lumen, often appearing packed, distinctly greyish, 10–19 per median leaf cell, coarsely papillose, the spherules soon swelling and coalescing and the oil-bodies then increasing botryoidal, many oil-bodies globose, some el-

liptic, notably variable in size within a cell, some ± 3–4× smaller than others, some of larger ones at times with a crease or depression, the oil-bodies 5.8–7.7 × 10.1–12 μm, to 8–8.5 × 11–16 μm to 10–11 × 11–13 μm, spherical ones 4.8–8.2 μm in diam.

Androecia on abbreviated branches from stolons or bases of erect, leafy branches, pale, compactly spicate, often clustering, often coiled, often somewhat dorsiventrally compressed; bracts in 4–6 pairs, strongly and deeply saccate, the dorsal margin entire, the apex entire or irregularly crenulate, the marginal cells elongated at right angles to margin; antheridia 1 per bract, the stalk rather long, uniseriate; bracteoles present at least in basal half of androecium, scale-like, irregular in shape, the apex and often margins rather coarsely crenulate. Gynoecia similar in position to androecia, bulbous, fleshy and rhizoidous at base; bracts in 2–3(4) series, pale, the innermost (non-perianth-forming cycle) free from one another, conspicuously larger than those below, the apex irregularly spinose dentate-lobulate, the margins of the lamina dentate by 1–2-celled teeth, the terminal cell rather elongate, the lamina often subentire below; bracteoles subequal to bracts or somewhat smaller, at times much more so, at times reflexed; innermost series of bracts and bracteole (the perianth-forming cycle) extremely variable, at times united and developed as a distinct perianth, at times ± deeply divided and only basally connate, at times completely divided into separate, free bracts; perianth (when present) short, obscurely to rather distinctly trigonous, variable in shape, narrowly to broadly and stoutly ovate-cylindrical, with sharply lanceolate scales inserted on basal sector, often plicate, straight or more often narrowed toward the mouth, the mouth broad to narrow and contracted, the mouth (or, in absence of a perianth, the apex of the perianth-forming cycle of bracts) irregularly and densely spinose-ciliate, the cilia composed of a uniseriate row of 3–6 elongate, often thick-walled cells. Mature calyptra thin, membranous, 3–5-layered medially, collapsing distally after capsule dehiscence, extending to level of perianth mouth (when perianth present) or beyond, with sterile archegonia at calyptra base or if elevated then remaining in basal third, a few paraphyllia sometimes present at calyptra base (distal to bracteole).

Seta very long (to 3.5 cm long), seen only in collapsed state. Capsule ellipsoidal, the wall 54–64 μm thick, of 4–5 layers; outer layer of cells quadrate to short-rectangular, with imperfect two-phase development, the longitudinal walls with strong nodule-like thickenings alternating with primary walls either devoid of thickenings or with a few nodular thickenings, the transverse walls with thickenings absent or, often, present; innermost layer of cells for the most part irregularly narrowly rectangular, with semiannular bands, the bands narrow, sometimes incomplete, often forked and sometimes anastomosing to delimit local fenestrae, the longitudinal and transverse walls at times with nodule-like thickenings.

Spores 32.2–37.4 μm in diam. (including bacula), yellow-brown, baculate, the bacula rather widely spaced, slightly wider at base, truncate at the apex and often flared, the ground surface otherwise with a network of delicate, fine, narrow, rather distantly spaced low ridges, the ridges sporadically forked, the surface of ridges without papillae; spore:elater diam. ratio 3.5–4.1:1. Elaters somewhat adhering to inner face of capsule wall after capsule dehiscence, tortuous, 9.1–10.6 μm in diam., bispiral to tips or the ends at times somewhat attenuated and in that sector unispiral, the bands 2.9–3.4 μm wide.

Distribution and Ecology: New Zealand: Campbell Island (60 m), Auckland Islands (275–400 m), Stewart Island, South Island (180–1250 m), North Island ([50]300–1100 m), Chatham Islands; Australia: Tasmania, Victoria, New South Wales; New Caledonia, southern Chile, Juan Fernandez, Inaccessible Island, Nightingale Island. In New Zealand known from Fiordland,

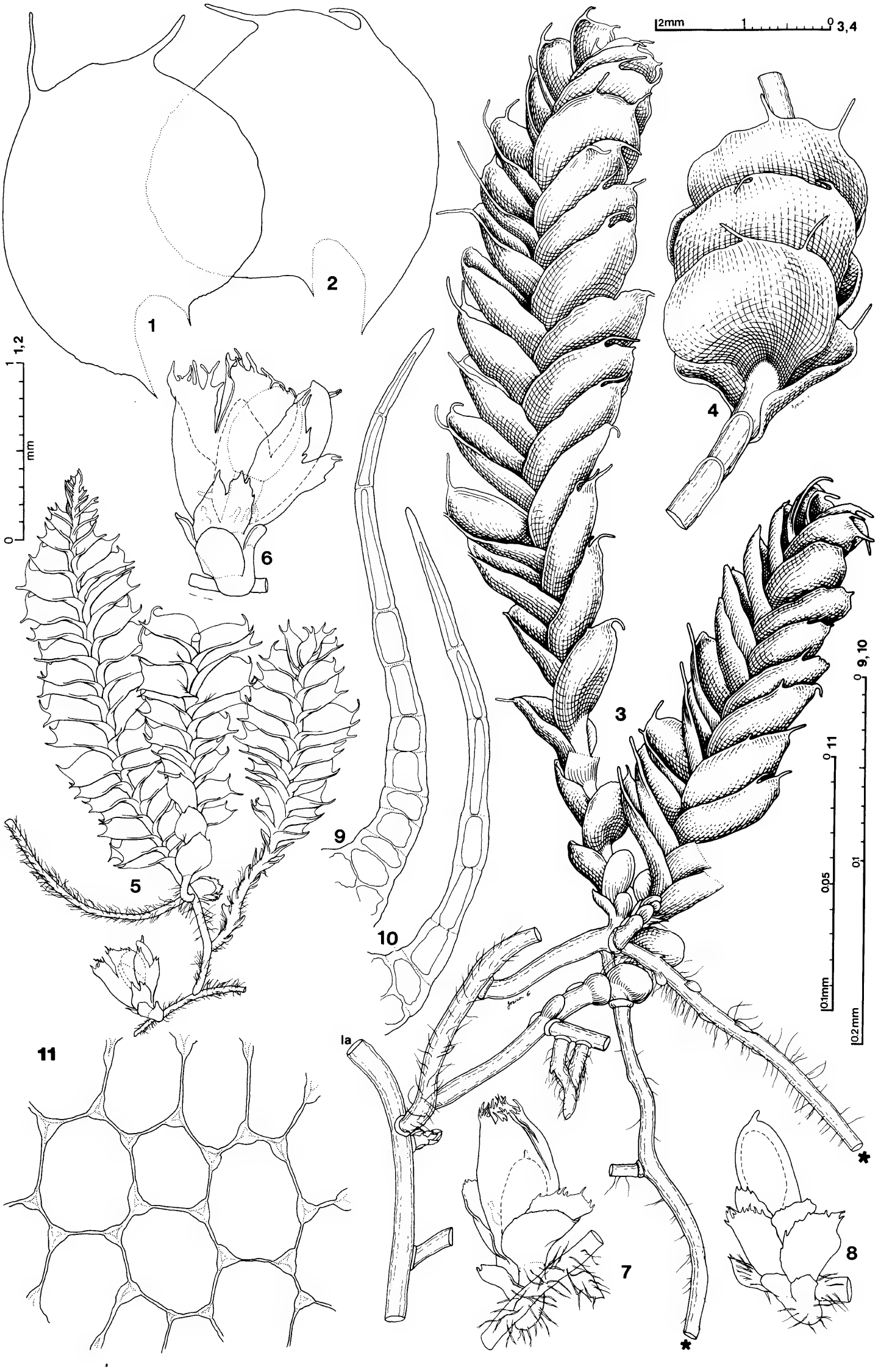

Fig. 129.
Pseudomarsupidium piliferum (Steph.) Herzog *ex* Grolle. 1, 2. Leaves. 3. Portion of plant showing system of copiously branched, prostrate stolons and erect leafy shoots (la = leafy shoot, which was

Westland, Western Nelson, Volcanic Plateau, Taranaki, Auckland (Mt. Moehau, Great Barrier Island) and Northland EPs.

In New Zealand occasional but not frequent. In the South Island in forests of *Nothofagus solandri* var. *cliffortioides* or of *N. menziesii* forest where it may form thick, often pure, mats over thin soil on cliff faces or on rock ledges of outcrops, or, less often, on bark of *Nothofagus*. In the North Island in scrubland or areas with low open stunted trees and shrubs, often in fairly exposed sites. It occurs epiphytic on trunks of *Kunzea ericoides* (with *Hymenophyllum* and *Bazzania hochstetteri*), or of *Weinmannia racemosa*, or (Mt. Moehau, ca. 840 m) on upper branches of stunted *Phyllocladus glaucus* in an area with stunted *W. silvicola*, *Coprosma foetidissima* and *Corokia buddleioides* or (Mt. Te Aroha, 950 m) on small upper branches of *Weinmannia* in a stunted mixed-age *N. menziesii*, *Weinmannia* and *Ixerba brexioides* forest. Other known hosts are *Brachyglottis rotundifolia*, *Leptospermum scoparium*, *Mida cunninghamii*, *Neomyrtus pedunculatus* and *Prumnopitys taxifolia*. In exposed sites tufts of the species are often a dull olive-brown or chestnut-brown. Also on ground at cliff bases or on weathered rock, at times associated with *Jamesoniella colorata* and *Cuspidatula monodon*. Also at a considerably lower elevation (50–160 m) on Rangitoto Island; the species occurred on a thick layer of soil over shaded rock in a *Metrosideros* forest developed over a lava flow. At Stockton Plateau it occurs in soil pockets in deeply eroded sandstone pavements among low *Leptospermum scoparium* and *Rytidosperma setifolium*, with *Acromastigum anisostomum*, *Campylopus clavatus*, *Cladonia confusa*, *Dicranoloma robustum*, *Holomitrium perichaetiale*, *Jamesoniella colorata*, *Rhacocarpus purpurascens*, *Siphula decumbens* and *S. fragilis*. At other sites on soil or rock it has also been found with *Anastrophyllum schismoides*, *Campylopus introflexus*, *Herbertus oldfieldianus*, *Hypnum chrysogaster*, *Lepicolea attenuata* and *Racomitrium pruinosum*. Where epiphytic it has been found with *Bunodophoron scrobiculatum*, *Chandonanthus squarrosus*, *Cuspidatula monodon*, *Dicnemon calycinum*, *Herbertus oldfieldianus*, *Heteroscyphus menziesii*, *Holomitrium perichaetiale*, *Jamesoniella colorata*, *Lepicolea attenuata*, *Leptostomum macrocarpum*, *Paraschistochila tuloides* and *Plagiochila circinalis*.

Comments: This strongly fuscous plant has ± transversely to succubously oriented, concave leaves with the dorsal margin stiffly elevated, and the leaf apex with 2 hyaline, stiff awns (rarely reduced and tooth-like). It is not likely to be mistaken for anything else, although it somewhat resembles species of *Marsupidium* in aspect, but these are green, and never have the blackish brown color of the *Pseudomarsupidium*.

The gynoecium of *Pseudomarsupidium piliferum* is variable in the extent of perianth development. The uppermost gyre of bracts and bracteole (the perianth-forming cycle) may be a) fused nearly to the summit, thus forming a distinct and well-defined perianth (Fig. 129: 7); b) connate only at the base, the perianth lobes thus being deeply divided (Fig. 129: 6); or c) completely free, a true perianth thus completely lacking (Grolle, 1972a, pl. 10 n). The calyptra is 3–5-stratose in the median sector and may be within the confines of the perianth (Fig. 129: 7) or exceed it (Fig. 129: 8; Fig. 130: 1). Figures 129: 7 and 8 were redrawn from Grolle

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removed). 4. Sector of leafy shoot (note leaf insertion), lateral view. 5. Plant with leaves widely spreading. 6–8. Gynoecial branches. 9, 10. Awns of same leaf apex. 11. Median leaf cells. (Figs. 1–4, from *Engel 14024*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park, Ballroom Forest; 5–8, after Grolle, 1972a; 9, 10, from *Engel 13798*, Tasmania, near Scotts Peak Road; 11, from *Norris 26966*, Tasmania, trail to Adamsons Peak.)

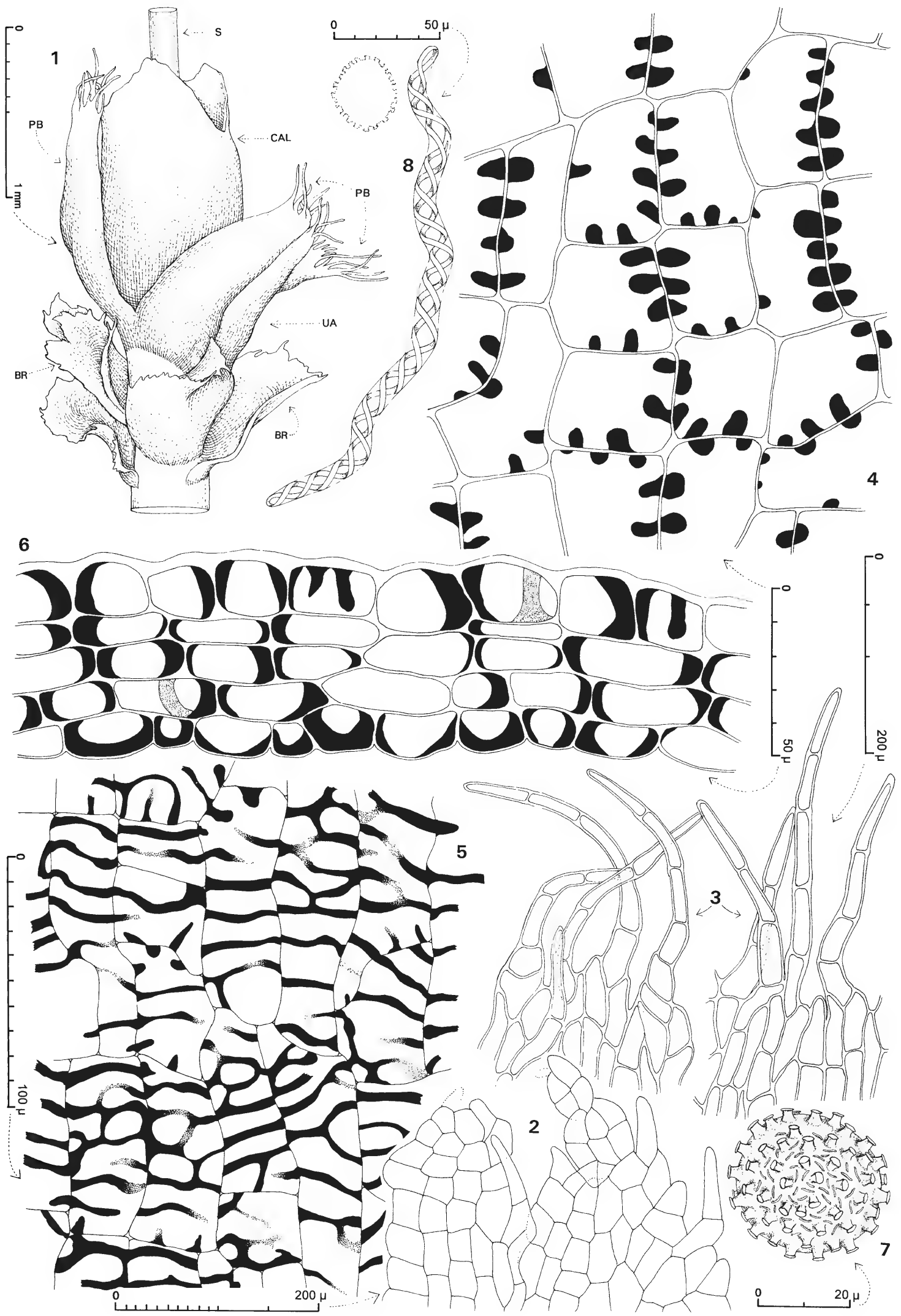

Fig. 130.
Pseudomarsupidium piliferum (Steph.) Herzog *ex* Grolle. 1. Gynoecium with mature sporophyte (ventral view); note that a tubular perianth is absent, the cycle of all 3 perianth-forming bracts (= PB) are subequal in size and are partially fused to one another, but are otherwise free above;

(1972a), who based them on the same collection (*Schwabe 53a* from Chile). *Engel 16275* from Tasmania has a well-developed perianth and a calyptra that extends to the perianth mouth. Shoots of *Braggins 99269A* (Mt. Taranaki, AK) have sporophyte-bearing gynoecia with the cycle of all 3 perianth-forming bracts fused to one another only at the extreme base, but are otherwise free above (Fig. 130: 1). The perianth-forming bracts are deeply concave to inflated-pouched, are weakly to distinctly longitudinally plicate (Fig. 130: 1) and are similar in appearance to plicate perianths in various other hepatic families. The perianth-forming bract apex has cilia with a uniseriate row of 3–6 elongate cells (Fig. 130: 3). Unfertilized archegonia are positioned at or near the base of the calyptra (Fig. 130: 1).

Pseudomarsupidium piliferum is yet another species exhibiting a suite of sporophyte and spore characteristics shared by unrelated taxa that are uniformly or mostly corticolous. For a discussion see Engel and Gradstein (2003).

Adelanthus Mitt.

Adelanthus Mitt., J. Proc. Linn. Soc., Bot. 7: 243. 1864, *nom. cons*. Type: *A. falcatus* (Hook.) Mitt.
Calyptrocolea R.M.Schust., Rev. Bryol. Lichénol. 34: 685. 1967 (1966). Type: *C. gemmipara* R.M.Schust.

Plants slender, rigid and wiry yet flexuous, deep green to ± deep brown to black with maturation, nitid, small to medium, to 2.4 mm wide; leafy shoots stiffly erect, arising from a ± intricate system of branching, rhizomatous axes. Branching normally exclusively intercalary, the branches normally arising ventrally or from ventral leaf angles low down on leafy shoots, never clearly axillary, either abruptly phototropic after their origin and then becoming leafy, or geotropic and then forming stoloniform axes commonly occurring just beyond point of origin of a leafy branch, the leafy and stoloniform axes mostly at 180° to each other; erect leafy axes usually unbranched above, rarely and sporadically with a *Frullania*-type branch distally. Stems rigid and wiry, usually fuscous pigmented and darker than the leaves, with cortical cells persistent and not collapsing (a hyaloderm lacking), in surface view strongly elongated (4–10:1), in cross section with a well-defined, (1)2–3-stratose cortex of small cells with extremely thick walls and reduced lumina. Rhizoids almost exclusively confined to stoloniform axes. Leaves nitid, usually vertically or subvertically oriented, the dorsal leaf surface inclined or appressed to axis, erect to erect-spreading, scarcely to weakly concave, the mature ones suborbicular to asymmetrically ovate to ovate-reniform; margins usually denticulate to serrulate, occasionally entire, the apices never bidentate, the dorsal margin often clearly incurved, never deflexed. Cells (except marginal and submarginal ones) rather small, oblong (mostly 1.5–3:1), grading into a basal region of strongly elongated cells (to 3–6:1) and with a ± well-

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note that the perianth-forming bracts are conspicuously plicate. Note also the 2 innermost bracts (= BR) + bracteole (facing viewer) below the perianth-forming cycle, and also the position of unfertilized archegonia (= UA at arrow) (CAL = calyptra; PB = bract of perianth-forming cycle; BR = bracts (true) of innermost cycle; S = seta). 2. Portion of apex of uppermost true bract (non-perianth-forming cycle). 3. Portions of apex of innermost bracts of perianth-forming cycle. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. 6. Capsule wall, cross section. 7. Spore. 8. Elater + spore outline (tuberculae included). (All from *Braggins 99269A*, New Zealand, North Is., Egmont Natl. Park, Mt. Taranaki, Potaema Track.)

defined vitta differentiated, the median and basal cells serially oriented, the upper cells thin-walled to firm-walled and lacking distinct trigones, the elongated basal cells with walls evenly thick-walled but without distinct trigones, the lumina rounded at the angles; cells of marginal 2–4 (or more) rows often thick-walled, subquadrate to short-rectangular with long axes usually oriented radially, forming a ± distinct border. Oil-bodies 3–9 per median cell, finally papillose to irregularly botryoidal. Underleaves reduced to 1–2 cells or absent. Asexual reproduction by 1–2-celled, elliptical to ovoid, green gemmae, formed at shoot apices from reduced leaves and/or geotropic axes.

Androecia confined to basal, very short, ventral-intercalary branches, whitish; bracts in 4–6 pairs, small, imbricate, unlobed or emarginate; antheridia normally 1 per bract. Gynoecia confined to basal, very short, ventral-intercalary branches lacking vegetative leaves; bracts in 2–4 gradually larger series or the innermost at times smaller, the innermost series delicate, weakly or not chlorophyllous, the apices unlobed or ± 2–3-lobed, the margins toothed; shoot-calyptra massive, ovoid-cylindrical at maturity, green, fleshy, with polystratose wall, the unfertilized archegonia present to at least the middle; perianth wholly lacking (except sect. *Pittieri*).

Capsule ovoid to ellipsoidal, the wall 4–6-stratose; outer layer of cells with strongly developed nodular (radial) thickenings, mostly confined to alternating longitudinal walls; innermost layer of cells with well-developed complete to incomplete semiannular bands.

Spores granulate or with vermiculate, rarely anastomosing ridges; spore:elater diam. ratio 1.4–1.7:1. Elaters bispiral, the spirals close, rather wide.

Type: *Adelanthus falcatus* (Hook.) Mitt. (≡ *Jungermannia falcata* Hook.)

A genus of 10 species. Section *Calyptrocolea* (R.M.Schust.) Grolle has three species, including the closely related species pair *Adelanthus tenuis* J.J.Engel & Grolle of the Falkland Islands, Tierra del Fuego, southern South America and *A. gemmiparus* of our area. The third species (*A. areomarginatus* R.M.Schust.) is Andean. Two of the three species of sect. *Lindenbergiani* Grolle also are Austral. *Adelanthus integerrimus* Grolle is subantarctic (Crozet Island, South Georgia, Falkland Islands, Tierra del Fuego and southern South America) and *A. lindenbergianus* (Lehm.) Mitt. is amphi-Atlantic-temperate, occurring on Mascarene Island, Réunion, Madagascar, South Africa, East African mountains, Tristan da Cunha, Inaccessible Island, South Georgia, Falkland Islands, Tierra del Fuego, southern South America, Juan Fernandez, and the Andes north to Mexico, and is disjunct in western Ireland and NW Scotland. The third species (*A. carabayensis* (Mont.) Grolle) is Neotropical. Section *Adelanthus* has two Australasian species, both occurring in our area. Section *Pittieri* Grolle has two species: *A. pittieri* (Steph.) Grolle of the high Andes and the mountains of Central America + Jamaica and *A. squarrosus* Grolle of Guyana (Mt. Roraima). The genus does not extend into tropical sectors of the Old World.

Adelanthus is also distinct from *Pseudomarsupidium* in several sterile gametophyte characters. Species usually develop gemmae; those of *Pseudomarsupidium* never. Plants of *Adelanthus* usually show a clear distinction between a fuscous to blackish stem and polished leaves; the stem has a 2–3-layered persistent cortex of strongly pigmented and greatly elongated cells with greatly reduced lumina vs. a weakly differentiated cortex formed of only moderately incrassate cells in *Pseudomarsupidium*. In *Adelanthus* the leaf shows strong regional cellular differentiation: the peripheral cells, in several rows, average small and subquadrate (1–1.2:1), grading into subapical and median cells that are rectangular to hexagonal-rectangular (to 3:1),

grading into a basal field of narrowly rectangular cells (to 6:1). Except at the leaf margins, cells are mostly oriented in lines or arcs and are often locally tiered. All cells are basically non-collenchymatous, the walls evenly thickened, the lumina remaining angular. These differences are much less marked in *A. gemmiparus*. Also, *Frullania*-type branching is developed in some taxa (e.g., *A. falcatus*); in *Pseudomarsupidium* terminal branching is completely lacking.

Descriptions are adapted, with much modification, from Schuster (1967c).

References: Grolle (1972a, rev.; 2003); Hodgson (1970, rev.); Schuster (1967c; 2002a).

Key to Species

1a. Mature leaves obliquely to widely spreading, subrotundate and nearly symmetrical, suborbicular, scarcely wider than long, edentate; basal leaf cells moderately elongated, 1.8–3:1; marginal cells in 3–4 rows, forming a weak border of somewhat thick-walled cells, subquadrate or radially elongated, contrasted to thinner-walled intramarginal cells; gemmae at shoot tips and on apices of stolons, 1-celled . . . . . *A. gemmiparus* (p. 617)

1b. Mature leaves erect to suberect, strongly asymmetrically reniform, decurved-homomallous, the ventral sector strongly ampliate, much wider than long, dentate or edentate; basal leaf cells narrowly rectangular to linear, 3–6:1; marginal cells thick-walled, ± quadrate in several peripheral rows; gemmae either absent or at shoot tips and 2-celled 2

2a. Leaves sharply serrate, at least distally, the larger broader than long, becoming much smaller-leaved on shoot apices and as long or longer than broad; shoot apices conspicuously cernuous to circinate; leafy shoots above with occasional branches, sometimes subdendroid; mature stems black; cell arrangement relatively irregular, the cells, except peripherally, oriented neither in rows nor arcs, with a distinct basal area weakly developed; gemmae lacking . . . . . *A. falcatus* (p. 621)

2b. Leaves edentate, similar-sized throughout, the upper not strongly reduced in size; shoot apices straight or at most decurved, not circinate; shoots above stoloniform base, almost uniformly unbranched; mature stems brown to fuscous; cell arrangement very regular, with strongly defined basal area; gemmae 2-celled . . . . . *A. occlusus* (p. 625)

Adelanthus gemmiparus (R.M.Schust.) E.A.Hodgs.

[Plate 12A; Fig. 131; Fig. 146: 1, oil-bodies, p. 672]

Calyptrocolea gemmipara R.M.Schust., Rev. Bryol. Lichénol. 34: 695. 1967 (1966). *Adelanthus gemmiparus* (R.M.Schust.) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Biol. Sci. 11: 241. 1970. Holotype: New Zealand, South Is., Westland, 0.6 miles below Haast Pass, ca. 1650–1700 ft., *Schuster 53384* (herb. Schuster, *non vidi*); isotype: (G!).

Plants forming ± interwoven mats, the ± rigid leafy shoots erect, sparingly branched, straight and not cernuous, of limited length, arising from a creeping and descending system of leafless, rhizoidous axes, or from basal sectors of eventually leafy stems, olive-green to deep green, nitid, the stems ± brownish but never blackish with age, the plants small, to 1450 μm wide. Branching exclusively ventral- and lateral-intercalary (from ventral angle of lateral leaves), the leafy branches arising at ± right angles to parent axis but soon abruptly genicu-

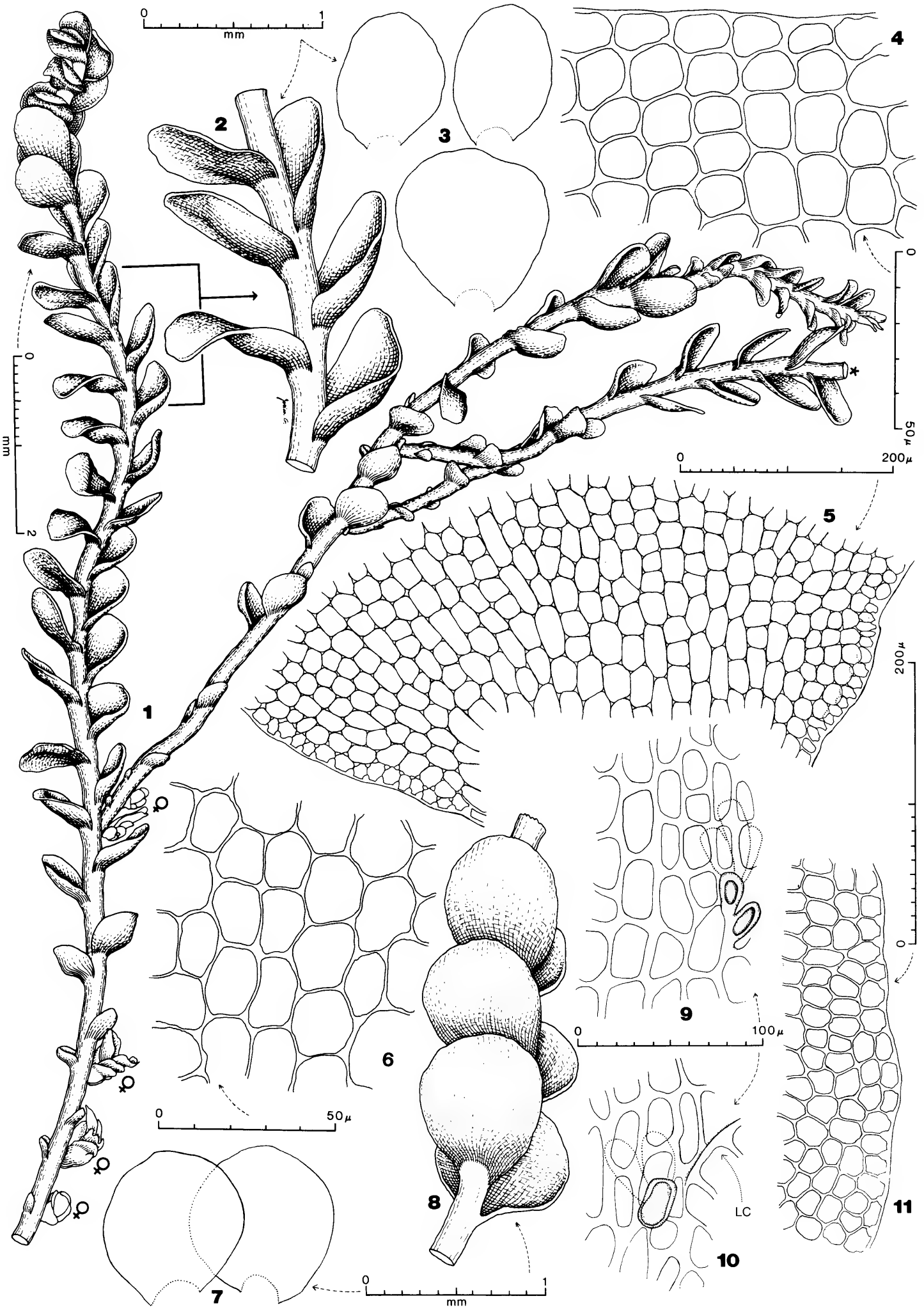

Fig. 131.
Adelanthus gemmiparus (R.M.Schust.) E.A.Hodgs. 1. Erect leafy shoot with basal gynoecia, dorsal view. 2. Sector (indicated by bracket) of shoot shown in fig. 1, dorsal view. 3. Three leaves (drawn to same scale). 4. Portion of leaf apex. 5. Leaf base. 6. Median leaf cells. 7. Leaves. 8. Sector of leafy shoot, lateral view. 9, 10. Stem cells and underleaves, at top the underleaf consists of a pair of laterally juxtaposed cells and associated slime papillae, at bottom of 1 cell and slime papillae (LC = leaf cell). 11. Median sector of leaf margin. (All from *Norris 28517*, Tasmania.)

late and becoming erect, often with a brownish, vestigially leaved geotropic stolon arising just above the point of origin of the eventually leafy axis. Stems rigid, the cortical cells very thick-walled, in 2(3) strata, in surface view narrowly rectangular, their lumina reduced and rounded in cross section. Leaves rather stiffly and widely patent, distichous, distant, subtransversely oriented, the insertion almost transverse dorsally but succubous elsewhere, inserted to stem midline dorsally, slightly concave at the base, elsewhere nearly flat and somewhat squarrose, equal-sized, symmetrical, almost orbicular to broadly oval or feebly obovate, longer than wide at least in median sector of shoots, the leaves 375–390 μm wide × 400–410 μm long to 725–750 μm wide × 725–815 μm long; margins entire except for the faint crenulations formed by the protuberant radial walls of marginal cells, the marginal cells often forming a weakly elevated border. Cells of lamina ± thin-walled but with moderate to rather conspicuous, concave- or weakly convex-sided trigones, the subapical cells 17–23 μm wide and long, the median cells 15–18 × 16–22 μm; basal cells not forming a distinct field, the cells relatively weakly elongated, 14–20 × 25–45 μm (2–3:1); marginal cells 10–15 μm and subquadrate or a little elongated at right angles to margin, trigones weak, concave-sided, the cells in marginal 3–4 rows forming an indistinct border, the radial walls swollen externally and dilated, the leaves thus feebly crenulate; surface smooth. Oil-bodies occupying a conspicuous part of the cell, greyish at lower magnification, dull opaque very pale grey at higher magnification, (2)3–4(5) per median leaf cell, finely papillose, the spherules protruding beyond the membrane. Chloroplasts large for cell size. Underleaves inconspicuous and easily overlooked, reduced to 2–3 slime papillae subtended by 1 or a pair of laterally juxtaposed, thick-walled cells. Asexual reproduction by 1-celled, pale to greenish, thin-walled gemmae, either from margins of leaves and 10–11 × 12–16 μm, or from apices of geotropic axes and 7.5–9 × 11–16 μm.

Androecia very compact, small, ± hyaline, arising from bases of ventral branches or stolons; bracts strongly concave, imbricate, in 4–6 pairs, unlobed, hyaline or subhyaline, in part margined as in leaves, faintly crenulate, the marginal cells elongated at right angles to margin; antheridia 1 per bract. Gynoecia on short, ventral branches that are initially somewhat spreading but become abruptly arched and erect; bracts and bracteoles in (2)3–4 gyres, those below small, scale-like, enclosing the innermost gyre of bracts and bracteoles; innermost bracts ovate or ovate-pointed, bidentate to shortly bifid or the arched dorsal margin with 2(3) small, erect, ± denticulate lobules, the margins sparingly setulose-ciliate or setulose-denticulate above with variable teeth, in part merely projections of upper ends of cells; bracteole large, with margins like bracts, but lanceolate-pointed, apiculate with 2–3 superposed cells. Shoot-calyptra erect, green, thick-walled, 1150–1300 μm long, bearing on its surface unfertilized archegonia and scattered, irregular few-celled, loosely attached papillae. Perianth lacking.

Capsule (known only immature) with 4–6-stratose wall. Elaters bispiral.

Distribution and Ecology: New Zealand: Stewart Island, South Island (610–1200 m), North Island (760–1320 m); Australia: Rare in Tasmania (Engel, 1991c). Known from Otago, Westland, Canterbury (Arthur's Pass), Western Nelson, Gisborne and Volcanic Plateau EPs.

This rather small and nondescript species has a sporadic distribution and is usually found in moist, deeply shaded situations often on wet peaty banks or on peat-covered rock. At Bridal Veil Track (Arthur's Pass, E side of Bealey River, 760–825 m), occurring mixed with *Eotrichocolea polyacantha* at the base of a pocket of a vertical mossy bank in a forest dominated by *Nothofagus solandri* var. *cliffortioides* with some *Griselinia littoralis* and *Pseudopanax*. At the Owen River found under *Nothofagus fusca* forest on a soil bank, with *Pyrrhobryum mnioides*, *Schizymenium bryoides* and *Tylimanthus diversifolius*. Also known from a stream

bank at Temple Basin (Arthur's Pass, 760 m), in *Chionochloa pallens* tussockland on the Wilberg Ra. (central Westland, 1030 m) and on Mt. Misery (Otago, 610 m). The type occurred 1 km west of Haast Pass. Also known from a few stations in the North Island. At the summit area of Te Rangaakapua (Huiarau Ra., Urewera Natl. Park, 1320 m) forming an extensive pure thick mat on a vertical rock wall in a mossy forest dominated by *Nothofagus menziesii* with some *Olearia colensoi*. Also at the margin of Lake Waikareiti (Urewera Natl. Park). Schuster (1967c, p. 697) recorded the species from soil over rock on the slope of Mt. Taranaki, at 1370–1525 m, in the *Chionochloa – Hebe* transition between alpine tussockland zone and penalpine scrub, on a moist rock wall with *Hymenophyllum multifidum*. Also growing with *Herzogianthus vaginatus* over a deep humus layer on a bryophyte-covered cliff face above the Mangawhero River (near Ohakune Mtn. Road, Tongariro Natl. Park) in an open, low *Nothofagus solandri* var. *cliffortioides* forest with *Libocedrus bidwillii*.

Other species that have been found with *Adelanthus gemmiparus* are *A. occlusus*, *Categonium nitens*, *Chiloscyphus mittenianus*, *Jamesoniella colorata*, *Kurzia hippuroides*, *Lepidogyna hodgsoniae* and *Lepidozia obtusiloba*.

Comments: In the field, the aspect of the plant is distinctive: the erect leafy shoots rarely exceed 10 mm high, with a tendency to grow as isolated, well-spaced, unbranched axes (the extensive system of ramified leafless axes scarcely evident), and the green to deep green color of the remote, rather stiffly spreading leaves, the stems at most light brown. When the plants are dissected out, the extensive system of geotropic stolons, arising from brownish lower sectors of stems, is evident. Some of these long and slender geotropic axes terminate in 1–2 small, reduced scale-like leaves that enclose an intensely green mass of gemmae.

As in other *Adelanthaceae*, the intercalary branches, arising either from the ventral angle of lateral leaves, or appearing to be truly ventral, are initially leafless and become abruptly erect prior to initiation of leaves. Just above their origin, such eventually leafy branches almost always form geotropic, leafless axes, the two branches aligned at 180° to each other.

Adelanthus gemmiparus is closely allied to *A. tenuis* J.J.Engel & Grolle of southernmost South America and the Falkland Islands (see comments in Schuster, 2002a).

Adelanthus gemmiparus may be confused with *Hepatostolonophora rotata* var. *perssonii* (R.M.Schust.) J.J.Engel (≡ *Calyptrocolea perssonii* R.M.Schust.), which is similar in size and has similarly oriented, suborbicular, obliquely to widely spreading leaves. This species also develops stoloniform geotropic axes, but these clearly arise in the axils of lateral leaves. In *A. gemmiparus* the stolons are brownish, at least with age, whereas in *H. rotata* they are purplish-tinged distally; the former lacks underleaves and has oil-bodies in all leaf cells, the latter has small, appressed underleaves and dimorphic cells, some with, some without oil-bodies. In cases of doubt, the peculiar differentiated leaf margins of *A. gemmiparus* are diagnostic: the radial walls of the marginal cells have dilated outer edges, so that leaves appear weakly and remotely crenulate.

Since several genera contain *Adelanthus gemmiparus* "look-alikes," a careful search for gynoecia or androecia should be made for generic confirmation.

Adelanthus falcatus (Hook.) Mitt.

[Plate 12E; Figs. 132, 133]

Jungermannia falcata Hook., Musci Exot. 1: *tab. 89.* 1818, *non J. falcata* Raddi, Jungermanniogr. Etrusca 22. 1818 [≡ *Diplophyllum albicans* (L.) Dumort.]. *Plagiochila falcata* (Hook.) Gottsche, Lindenb. & Nees, Syn. Hepat. 649. 1847, *non P. falcata* Steph., Sp. Hepat. 2: 248. 1902. *Adelanthus falcatus* (Hook.) Mitt., J. Proc. Linn. Soc., Bot. 7: 243. 1864. *Odontoschisma falcata* (Hook.) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 419. 1877. *Calyptrocolea falcata* (Hook.) R.M.Schust., Rev. Bryol. Lichénol. 34: 689. 1967 (1966). Type: New Zealand, South Is., Dusky Bay, 1791, *Menzies* (G!).

Plagiochila pusilla Mont., Ann. Sci. Nat. Bot. II, 19: 246. 1843. *Jungermannia pusilla* (Mont.) Hook.f. & Taylor, London J. Bot. 3: 578. 1844, *non J. pusilla* L., Spec. Pl. ed. 1. 1136. 1753. Type: Nova-Hollandia, Tasmania (= Van Diemen), *sin. coll.*, "ex Herb. Mus. Paris, ex Montagne" (G!).

Plagiochila intermixta Colenso, Trans. & Proc. New Zealand Inst. 21: 49. 1889 (1888). Type: New Zealand, Dannevirke, 1888, *Colenso*.

Plagiochila subpetiolata Colenso, Trans. & Proc. New Zealand Inst. 21: 49. 1889 (1888). Type: New Zealand, Whakatane Co., near L. Waikare, 1887, *Hamilton*.

Marsupidium capillare Berggr., On New Zealand Hep. 36. *f. 25.* 1898. *Plagiochila capillaris* (Berggr.) E.A.Hodgs., Trans. Roy. Soc. New Zealand 85: 581. 1958, *non P. capillare* Schiffn. *in* Steph., Sp. Hepat. 6: 137. 1918. *Adelanthus capillaris* (Berggr.) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 77. 1965. Type: New Zealand, South Is., Canterbury Prov., Castle Hill, *Berggren 3156*.

Plagiochila appressifolia Steph., Sp. Hepat. 6: 124. 1917. Holotype: New Zealand, Mamaku, 600 m, "Ende April 1903," *Fleischer 65* (G!).

Plagiochila inaequalis Steph., Sp. Hepat. 6: 169. 1918. Holotype: New Zealand, Mt. Winterslow, *Beckett 484* (G!); isotype: (CHR 585839 ex herb. Beckett!).

Plants with erect leafy shoots arising from a copiously ramified system of leafless, rhizoidous axes, gradually smaller-leaved to leafless and freely ramified below, the leafy shoot tips smaller-leaved, tapered, strongly cernuous to circinate, the leaves pure green and nitid, the stems becoming black and opaque with maturity, the plants medium-sized, to 2.5 cm tall. Branching ventral-intercalary or from ventral bases of lateral leaves, rarely and sporadically the leafy shoot furcate, with a terminal, *Frullania*-type branch; intercalary branches also occasional from distal half of leafy shoots, the leafy shoot system (optimally) subdendritic; leafless axes interwoven, intricately branched; ventral branches, eventually leafy and phototropic, usually bearing a creeping or geotropic axis just above their point of origin. Stems typically stiff and wiry, smooth, the cortical cells in 2 layers, small, fuscous-walled, very thick-walled, their lumina very narrow or almost obliterated on lower parts of axes, the outer medullary cells often a little firm-walled, grading into a central medulla of thin-walled hyaline cells, but with ± thickened angles seen in cross section. Leaves ventrally secund (in lateral aspect of shoot half or more of leaf lying below the imaginary midline of stem), erect to suberect, vertical, the larger leaves imbricate as seen in lateral aspect, subtransversely oriented, strongly asymmetric, orbicular-ovate to subreniform-ovate, broader than long, the ventral portion distinctly ampliate, 1000–1200 μm wide × 850–900 μm long, to 1525–1550(1650) μm wide × 1125–1150 (1520) μm long, the leaves gradually becoming much smaller toward the circinate apices; margins broadly rounded above, with numerous unequal but small teeth separated by lunate sinuses (only rarely weakly toothed), the teeth extending to within 0.3 of leaf base but lacking from the dorsal margin, on larger leaves the teeth or serrations irregular, 40–50, broad-based, sometimes coarse and jagged; upper leaves smaller, obovate, often becoming longer than

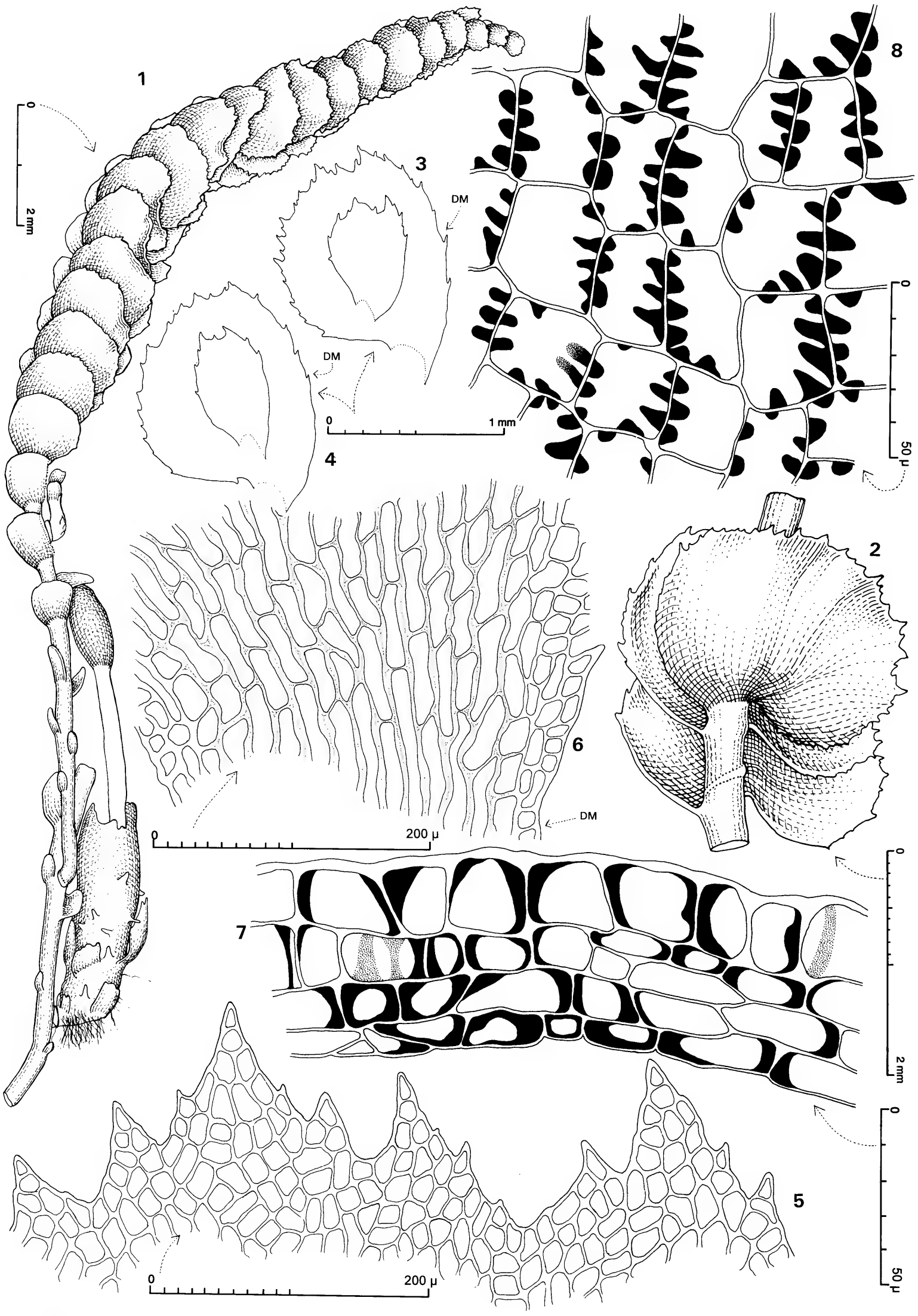

Fig. 132.
Adelanthus falcatus (Hook.) Mitt. 1. Sporophyte-bearing plant. 2. Sector of erect leafy branch, lateral view. 3, 4. Leaves (DM = dorsal margin) and within, a leaf from distal, attenuated region of shoot. 5. Distal sector of leaf. 6. Basal sector of leaf (DM = dorsal margin). 7. Capsule wall, cross

broad, almost symmetrical, with only 12–20 serrations. Cells firm-walled, lacking trigones and wall pigments, those in peripheral leaf sectors ranging from ± quadrate to obliquely quadrate or diamond-shaped, tending to lie in concentric arcs, forming longitudinal lines; marginal and submarginal cells 15–20 μm wide, thick-walled, gradually grading into the median cells; subapical cells 19–26 μm wide and long, the median cells with walls somewhat thinner than both subapical and marginal cells, the lumina more rounded at angles (vestigial trigones distinct), 15–21 μm wide × 20–35 μm long, varying from short-oblong to oblong-hexagonal or diamond-shaped; extreme base with an ill-defined region of elongated cells, above insertion 15–23 μm wide × 42–58 μm long (2.5–4.5:1), not forming a distinct area basalis, with sinuously thickened longitudinal walls; surface smooth. Oil-bodies dull opaque, pale smokey grey, with a milky appearance, 6–9 per median leaf cell, obscurely and indistinctly finely papillose, variable and often irregular in shape: globose to elliptic to sublinear to subcrescentic, some deltoid in profile, most 2.4–3.8 × 5.8–7.7 μm and a few 2.9 × 4.8 μm, globose ones 3.4 μm in diam. Underleaves lacking, the ventral merophytes 2–4 cells broad. Asexual reproduction not seen. Fungal partner an ascomycete.

Androecia on abbreviated branches from stolons or bases of erect, leafy branches, compactly spicate, very small, often clustered, often coiled, often somewhat dorsiventrally compressed; bracts in 4–6 pairs, strongly and deeply saccate, the dorsal base strongly involute, the apices remotely and irregularly denticulate by the variously projecting apical ends of marginal cells, the marginal cells elongated at right angles to margin; antheridia 1(2) per bract, the stalk long and coiled. Gynoecial branches often clustered, developing a cylindrical-ellipsoidal to dumbbell-shaped, fleshy, green, thick-walled perigynium, 2.6–2.8 mm long and 925–975 μm in diam., at base with scattered, reduced small bracts and bractlets; bracts orbicular-ovate, unlobed or 2–3-lobed, serrulate to spinose-ciliate, the innermost bracts reduced in size.

Seta massive, with numerous rows of outer cells. Capsule ellipsoidal, the wall 56–70 μm thick, of 4–6 layers; outer layer of cells quadrate to short-rectangular, the radial walls with broad, strongly developed, nodular to spine-like thickenings that tend to be best developed on alternating longitudinal walls, the thickenings sometimes on transverse walls; innermost layer of cells with semiannular (to sometimes annular) bands common, narrow, at times incomplete, sporadically forked.

Spores 13–15.4 μm in diam., red-brown, with dense, low but sharply defined, close papillae and short simple or sometimes furcate vermiculate markings. Elaters ± tortuous, short and stout, 7.7–9.6 μm wide, only 86–120 μm long, moderately tapering to tips, bispiral, the spirals 2.4–2.9 μm wide.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands (Fineran, 1971), Stewart Island (100–475 m), South Island (120–1680 m), North Island (290–700 m); Australia: Tasmania, New South Wales. In New Zealand known from Fiordland, Otago, Canterbury (Hooker Valley, Arthur's Pass, Cass), Westland, Western Nelson, Volcanic Plateau, Taranaki, Gisborne and Northland EPs.

Common in densely forested areas over a rather broad altitudinal range (0–1680 m), often under *Nothofagus* (*N. solandri*, *N. menziesii*) and *Dacrydium cupressinum* forests. In such

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section. 8. Capsule wall, outer layer. (Figs. 1, 7, 8, from *Norris 27836*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park; between Lake Solitude to Little Hugel; 2, from *Engel 13904*, Tasmania, Weindorfers Forest; 3–6, from *Engel 23633*, New Zealand, North Is., Auckland EP, Kaimai-Mamaku Forest Park, Aongatete R.)

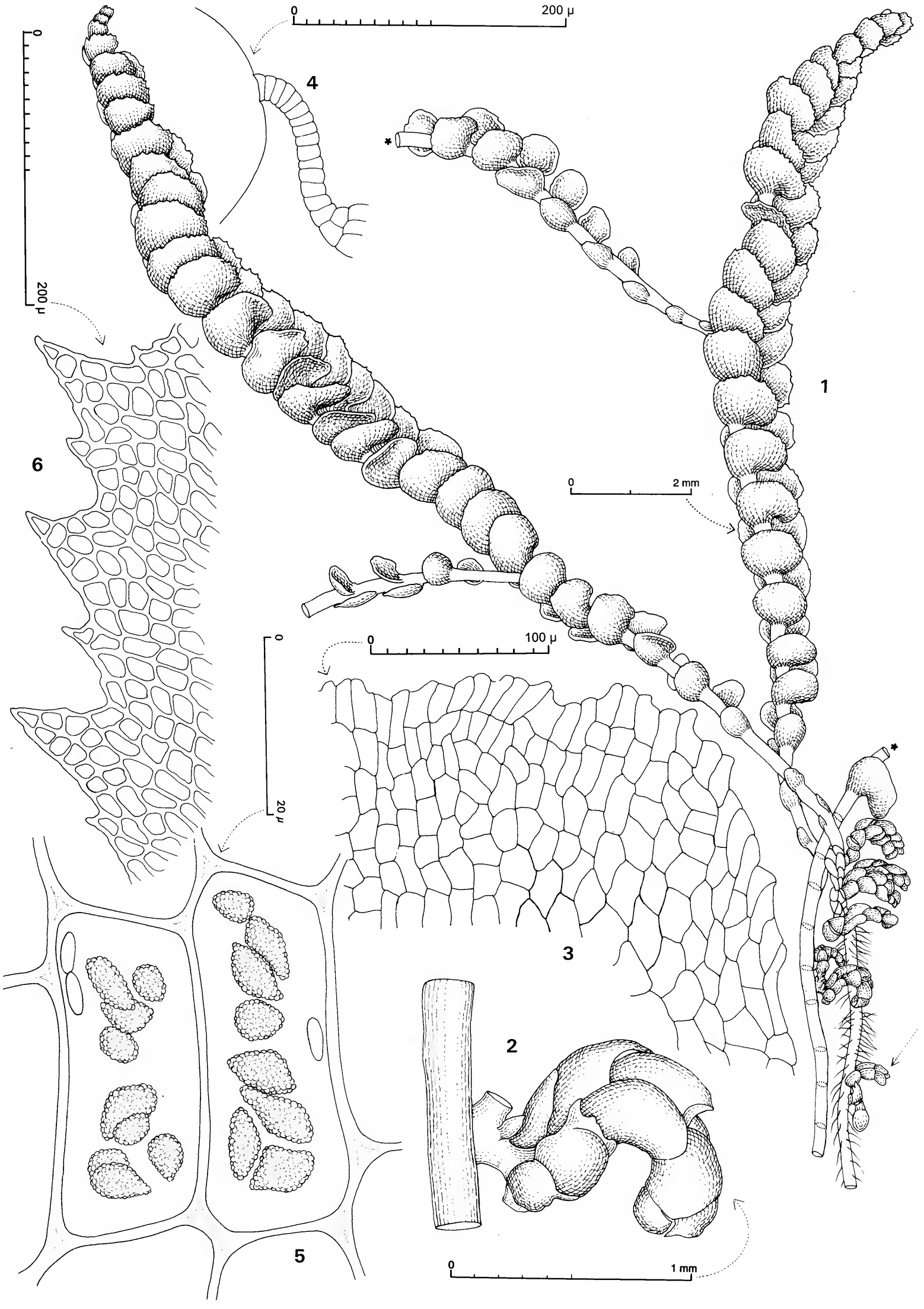

Fig. 133.
Adelanthus falcatus (Hook.) Mitt. 1. Plant with numerous basal androecia (* = position of severed leafy shoots). 2. Detail of the androecial branch indicated by arrow in fig. 1. 3. Portion of distal sec-

forests, it often is a component of the bryophyte-rich vegetation of the forest floor, where it may be a characteristic and abundant species. It is often found on stream banks, on gravel, stones, or boulders, or in seepage near stony-bedded streams. It is also rather frequent on rotted logs. It is found with *Breutelia elongata*, *Canalohypopterygium tamariscinum*, *Cryptochila grandiflora*, *Dicranoloma billardierei*, *D. robustum*, *Geocalyx caledonicus*, *Heteroscyphus cymbaliferus*, *H. sinuosus*, *Trichocolea mollissima*, *Tylimanthus saccatus* and *Wijkia extenuata*.

Comments: A characteristic and easily recognized species, distinct in the contrast between black, smooth, wiry stems and nitid, clear green leaves with conspicuous dentition. Equally distinctive are the ventrally decurved, almost hamate or coiled branch apices, which have progressively smaller and narrower leaves.

Sexual branches are freely produced in this species. However, they arise so far down, hidden by distal portions of plants and by accumulated debris, that they may be easily overlooked.

Adelanthus occlusus (Hook.f. & Taylor) Carrington

[Fig. 134; Fig. 146: 2, oil-bodies, p. 672]

Jungermannia occlusa Hook.f. & Taylor, London J. Bot. 3: 369. 1844. *Alicularia occlusa* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 619. 1846. *Adelanthus occlusus* (Hook.f. & Taylor) Carrington, Trans. Bot. Soc. Edinburgh 10: 381. 1870. *Odontoschisma occlusum* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 419. 1877. *Jamesoniella occlusa* (Hook.f. & Taylor) Steph., Sp. Hepat. 2: 102. 1901. *Calyptrocolea occlusa* (Hook.f. & Taylor) R.M.Schust., Rev. Bryol. Lichénol. 34: 692. 1967 (1966). Type: Campbell Is., *Hooker*.

Plants erect, caespitose, similar to *Adelanthus falcatus* but a little larger, the leafy shoots stiffly erect, simple or rarely branched, the shoots at most weakly cernuous at the extreme tips, the leaves similar in size and form above (except when gemmae are produced), the stems brown to fuscous but not black (except with decay), the leafy shoots to 5(6) cm tall. Branching all intercalary; leafy shoots arising from lowermost sectors of earlier generations of leafy shoots, from their leafless bases, or from stoloniferous axes and/or geotropic axes. Stems with cortex (1)2(3)-stratose, of very thick-walled, oblong to narrow-oblong cells. Leaves erect or suberect to appressed laterally to stem, vertically or subvertically oriented, decurved-homomallous, contiguous to (in lateral aspect) imbricate, the insertion nearly transverse in dorsal half, almost flat apart from a ± concave basal region, asymmetrically broadly reniform, broader than long, the ventral "half" extraordinarily ampliate, ± auriculate at base, the leaves strongly constricted to the narrow base, 1425–1500 μm wide × 925–950(1120) μm long to 1825 μm wide × 1140 μm long, the margins usually completely entire, rare and sporadic leaves with a few isolated small teeth, especially on distal leaves. Cells oriented in very regular lines, radiating fan-like from the contracted base, the cells very small and thick-walled in peripheral and apical sectors, 13–23 μm wide and long, gradually decreasing to 12–15 × 16–24 μm medially;

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tor of ♂ bract. 4. Antheridial stalk. 5. Median cells with oil-bodies. 6. Median sector of ventral margin of leaf. (Figs. 1, 2, from *Engel 14135A*, Tasmania, just W of Watersmeet, W of SW end of Lake St. Clair; 3, 4, from *Schuster 55486*, New Zealand, South Is., Fiordland EP, Cascade Creek; 5, from *Glenny 9599*, New Zealand, South Is., Western Nelson EP, Stockton Plateau; 6, from *Engel 23633*, New Zealand, North Is., Auckland EP, Kaimai-Mamaku Forest Park, Aongatete R.)

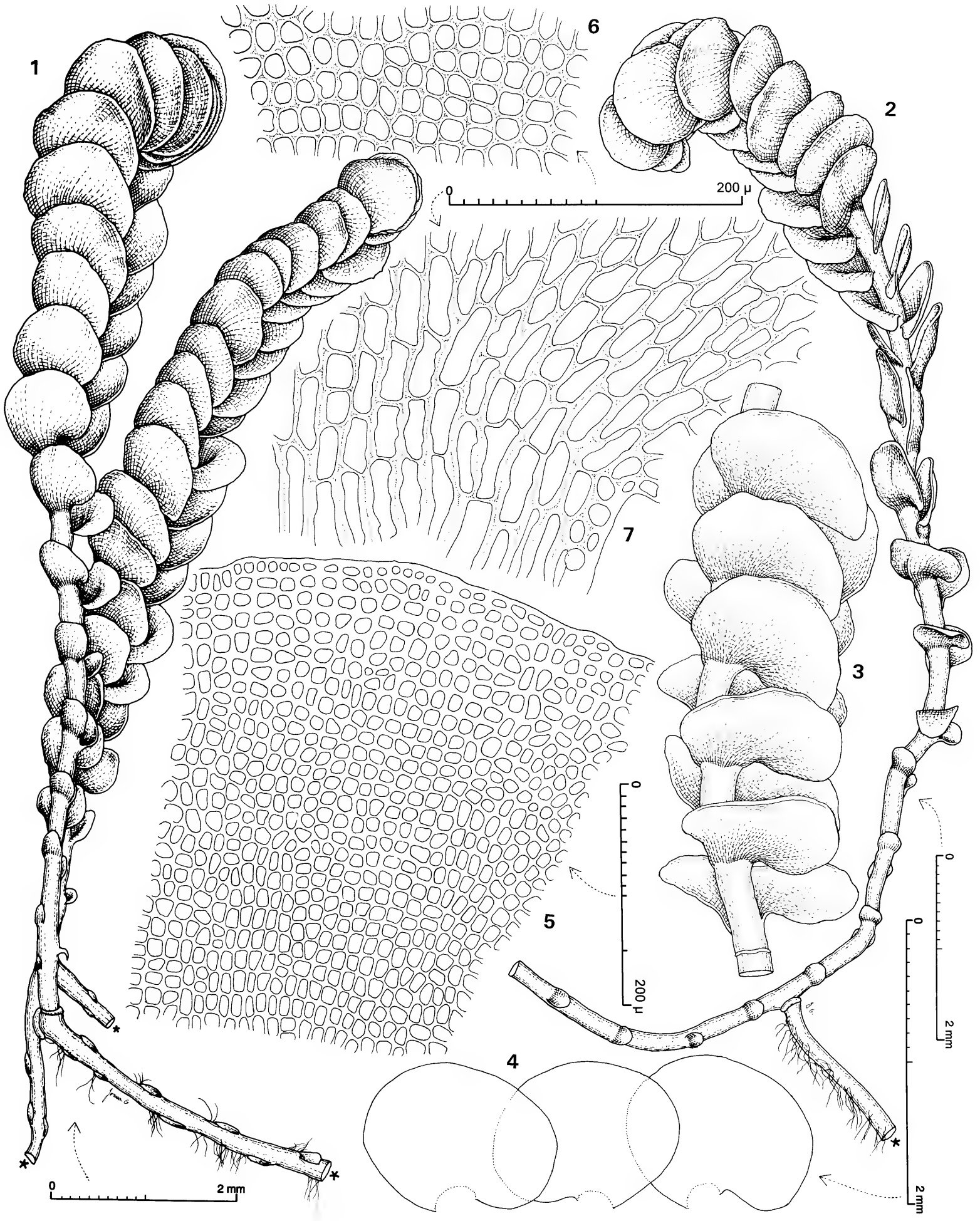

Fig. 134.
Adelanthus occlusus (Hook f. & Taylor) Carrington. 1. Erect leafy shoots and, at base, stolons, lateral-dorsal view. 2. Erect leafy shoot. 3. Sector of erect, leafy shoot, lateral view (drawn at same scale as fig. 4). 4. Leaves. 5. Median-distal sector of leaf showing cell arrangement in ± regular rows and tiers. 6. Median cells of leaf. 7. Basal cells of leaf. (Figs. 1, 2, from *Engel 16257*, Tasmania, SE of Black Bluff; 3–7, from *Engel 24285*, New Zealand, Stewart Is., Mt. Rocky summit area.)

basal cells forming a field of strongly elongated cells, 15–21 μm wide × 36–48(60) μm long to 13–16 μm wide × (38)40–54(66) μm long (3–3.5:1), with the longitudinal walls thick and often sinuous; surface smooth. Oil-bodies occupying a conspicuous portion of the cell lumen, dull opaque, with a cloudy appearance, 3–6(7) per median leaf cell, obscurely and irregularly botryoidal, the spherules protruding beyond the membrane. Underleaves lacking. Asexual reproduction via gemmae, these only at tips of leafy shoots, 2-celled, ellipsoidal, green, 13–14 × 18–23 μm to 15–16 × 18–21 μm and somewhat thick-walled.

Androecia unknown. Gynoecia on ventral, slight basitonic branches; bracts small, hyaline, the inner ovate, bilobed, the lobes crenulate-denticulate; shoot-calyptra fleshy, cylindrical-clavate, 2.2–2.4 mm long, 700–725 μm in diam., with unfertilized archegonia chiefly in basal 0.2–0.25. Perianth totally lacking.

Capsule ovoid, the wall 38–42 μm thick, of 4–5 layers; outer layer of cells with alternating (secondary) longitudinal walls with strong nodular thickenings; intermediate layers with strong nodular (radial) bands somewhat or strongly tangentially extended; innermost layer with strong, complete to incomplete semiannular bands, often complete also on internal walls (annular).

Spores 13.5–15.5 μm in diam., brown, the spore wall bearing low, delicate, simple or sometimes furcate vermiculate markings that usually fail to anastomose. Elaters 8–8.5 μm in diam., moderately attenuate at ends, bispiral, the spirals 3 μm thick.

Distribution and Ecology: New Zealand: Campbell Island (70–310 m), Auckland Islands (70–560 m), Antipodes Islands (150–400 m), Stewart Island (500–1000 m), South Island (760–1200 m), North Island (760–1320 m); Australia: Macquarie Island, Tasmania, Western Australia. In New Zealand known from Fiordland, Westland, Western Nelson, Volcanic Plateau, Gisborne and Auckland EPs.

A species with a scattered and sporadic distribution but most abundant on the subantarctic islands. It occurs in *Nothofagus menziesii* and *N. solandri* var. *cliffortioides* forests, at times in masses of bryophytes over rotted wood or on steep, moist, peaty, mossy banks. Also on wet, peat-covered ledges or cliff faces, often where kept moist by seepage. On the Thousand Acres Plateau in the Matiri Ra. (Kahurangi Natl. Park, Western Nelson EP) occurring at ca. 1100–1200 m on the bank of a small still pool in a mosaic of *Chionochloa rubra* tussocklands, shrublands, *Phormium cookianum* tussocklands and *Celmisia monroi* herbfields. At the summit area of Te Rangaakapua (Huiarau Ra., Urewera Natl. Park) it occurred at 1265–1320 m on a nearly vertical bank at the margin of a wet depression in a mosaic of stunted *Olearia colensoi* and tussock with occasional *Coprosma* spp. At Mt. Moehau (summit area of "Little Moehau") it was found at ca. 850 m on a rock face of a large rocky outcrop in an area of very exposed bedrock with tufts of vegetation in protected pockets and crevices with windswept, dense scrub at the base, including *Leptospermum scoparium*, *Dracophyllum recurvum* and *Phyllocladus alpinus*. On Stewart Island occurring in a protected pocket with *Anastrophyllum schismoides* in mosaic communities of dense heath-forming shrubs to 3 m tall, penalpine herbs and dwarf heaths to 0.5 m tall, dominated by stunted *L. scoparium* and *Dracophyllum* and a ground tier including *Empodisma minus* (Mt. Rocky summit, 530 m). Also growing erect in a cushion of flowering plants in mosaic communities consisting of penalpine cushion vegetation, prostrate *L. scoparium* and *Olearia colensoi* to 1 m tall (Mt. Rakeahua, 500 m). Found with *Acromastigum anisostomum*, *Bazzania nitida*, *B. involuta*, *Chiloscyphus leucophyllus*, *C. spiniferus*, *Clandarium xiphophyllum*, *Dicranoloma billardierei*, *D. robustum*, *Eotrichocolea polyacantha*, *Gackstroemia alpina*, *Herbertus oldfieldianus*, *Heteroscyphus decipiens*,

Lepidozia hirta, *L. ornata*, *Marsupidium surculosum*, *Ptychomnion aciculare*, *Racomitrium crispulum*, *Schistochila monticola* and *Temnoma quadripartitum*.

Comments: A distinctive species that should not be confused with *Adelanthus falcatus*. Unlike *A. falcatus*, leaves are essentially entire-margined (Fig. 134: 1–4) and the shoot tips are never strongly coiled (Fig. 134: 1, 2); the uppermost leaves are reduced only when gemmae are produced.

Plants of *Adelanthus occlusus* have a *Plagiochila*-like appearance, and indeed closely mimic *Plagiochila retrospectans*, which may be very similar when it has subentire or minutely denticulate leaves. Weak forms of *P. retrospectans* and *A. occlusus* have a very similar facies, with leaves that are similar in shape. The leaves of these two species both have a border of small, thick-walled, subisodiametric cells, and a basal area of narrow, elongate cells. However, the subapical and median cells in *P. retrospectans* have very coarse, usually nodose trigones, and the dorsal leaf margins are somewhat deflexed, as in other *Plagiochila* species. In *A. occlusus* the dorsal margins are narrowly infolded or inflexed, as is normal for most *Adelanthaceae*. Also, the presence of gametangia, even when young, will immediately separate the *Plagiochila* on position of sex organs alone.

The erect, asymmetrically reniform leaves have a cell arrangement that is highly distinctive: the basal cells form an area of strongly elongated cells (3–3.5:1), with the longitudinal walls thick and often sinuous (Fig. 134: 7), grading into rectangular cells and then into submarginal and marginal cells that are more nearly quadrate and thicker-walled (Fig. 134: 5). Thus, the cells tend to be oriented in very regular lines, radiating fan-like from the contracted base (Fig. 134: 5).

Grolle (1972a) placed *Plagiochila orbiculata* Colenso in the synonymy of *Adelanthus occlusus*, but did not see the type. One of us (JJE) has seen the type specimen of *P. orbiculata* in the Geneva herbarium; it is *Plagiochila gigantea* (see also Inoue and Schuster, 1971, p. 190).

Wettsteinia Schiffn.

Wettsteinia Schiffn., Ann. Jard. Bot. Buitenzorg 2 (Suppl.): 44. 1898.

Plants usually pure green, lacking secondary pigments, the lower parts of stems white, the leafy shoots erect, arising from a system of plagiotropic, copiously branched, colorless, rhizoidous axes, the leafy shoots medium to vigorous, to 7 cm tall, the leafy shoots typically becoming smaller-leaved distally. Branching ventral-intercalary, arising from the stolons and lower sectors of leafy shoots; terminal branching absent. Stems with hyaloderm comprised of thin-walled cells that soon collapse and erode, the stem becoming roughened, the hyaloderm surrounding 3–5 strata of smaller, thick-walled, subepidermal cells that gradually grade into the hyaline, large-celled medulla. Rhizoids absent on leafy shoots. Leaves optimally developed only in median shoot sectors, smaller distally and below median sector, those of median sector 2–4-stratose toward base, remote to weakly imbricate, weakly to distinctly concave, ovate to obovate or orbicular-cordate, copiously dentate, the teeth larger and more remote on dorsal margin (lacking in *Wettsteinia densiretis*), smaller on apex and ventral margin. Cells in median sector of leaf with walls firm and at most moderately thickened or thin and with trigones at most weakly bulging, the basal cells only moderately elongated (to 60 μm), a vitta absent; marginal cells usually firmer-walled. Oil-bodies hyaline, 10–18 per cell in median sec-

tor of leaf, finely papillose. Underleaves vestigial, at times discernible on lower sectors of leafy shoots, ciliiform on upper shoot sectors. Asexual reproduction absent.

Plants dioecious. Androecia on strongly abbreviated intercalary branches from plagiotropic stolons, minute; bracts in 2–4 pairs, bleached, tiny, dense, inflated; antheridia 1(rarely 2) per bract, the stalk uniseriate. Gynoecia on strongly abbreviated intercalary branches from basal sectors of erect shoots or from plagiotropic stolons; bracts and bracteoles small, bleached, irregularly laciniate, comprised of thin-walled hyaline cells. Perianth absent. Shoot-calyptra rigid, fleshy, stoutly clavate, green, long-exserted beyond bracts, the sterile archegonia and at times a few bractlets elevated on the shoot-calyptra.

Foot conical, with a distinct haustorial collar. Seta massive. Capsule moderately long-ellipsoidal, the wall 6–8-stratose, the outer layer of cells mostly devoid of thickenings but some cells with nodular to spur-like thickenings on radial walls, the cells that possess thickenings sporadic and without a regular pattern of distribution; innermost layer of cells with semi-annular bands.

Spores with close papillae and very short-vermiculate markings. Elaters bispiral.

Type: *Wettsteinia inversa* (Sande Lac.) Schiffn. (≡ *Plagiochila inversa* Sande Lac.)

A genus of four species, two in Austral areas. *Wettsteinia densiretis* (Herzog) Grolle occurs in the Falkland Islands, southern South America (Valdivian) and Juan Fernandez, and *W. schusteriana* Grolle is found in our area. *Wettsteinia inversa* (Sande Lac.) Schiffn. occurs in New Guinea, Indonesia, Borneo, the Philippines and Taiwan, and *W. rotundifolia* (Horik.) Grolle is found in Taiwan.

References: Grolle (1965b); Schuster (2002a).

Wettsteinia schusteriana Grolle

[Plate 12F; Figs. 135, 136]

Wettsteinia schusteriana Grolle, J. Hattori Bot. Lab. 28: 99. *f. 2.* 1965. *Adelanthus schusterianus* (Grolle) E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 176. 1967. Holotype: New Zealand, South Is., Fiordland Natl. Park, Cascade Creek, *J. Burrell, G. A. M. Scott & J. Taylor* (CHR 135094!); isotype: (CHR ex herb. Allison H6526!).

Plants light green, the lower parts of stems whitish, the erect shoots typically leafless below, gradually larger-leaved above, the distal sector of shoot cernuous, with the leaves smaller and more densely imbricate, the plants vigorous, to 7 cm tall. Plants with a strongly developed system of basal, creeping, plagiotropic, often whitish stolons, from which arise erect, typically unbranched shoots; stolons and leafless sectors of erect axes giving rise to intercalary, geotropic, microphyllous, root-like axes, and also to intercalary, considerably more slender and whip-like secondary branches ("secondary roots"). Branching ventral-intercalary, arising from the stolons and lower sectors of leafy shoots. Stems comprised of a hyaloderm of 1–2 layers of numerous thin-walled, relatively small cells that collapse with age and 3–5 subepidermal strata of smaller, thick-walled cells that gradually grade into the large, hyaline, weakly firm-walled medullary cells. Rhizoids absent on leafy shoots. Leaves (optimally developed, in median sector of shoot) rather stiff and firmly attached to stem, ± clasping the stem, 2–4-stratose toward base, widely spreading but becoming inclined toward the stem and laterally

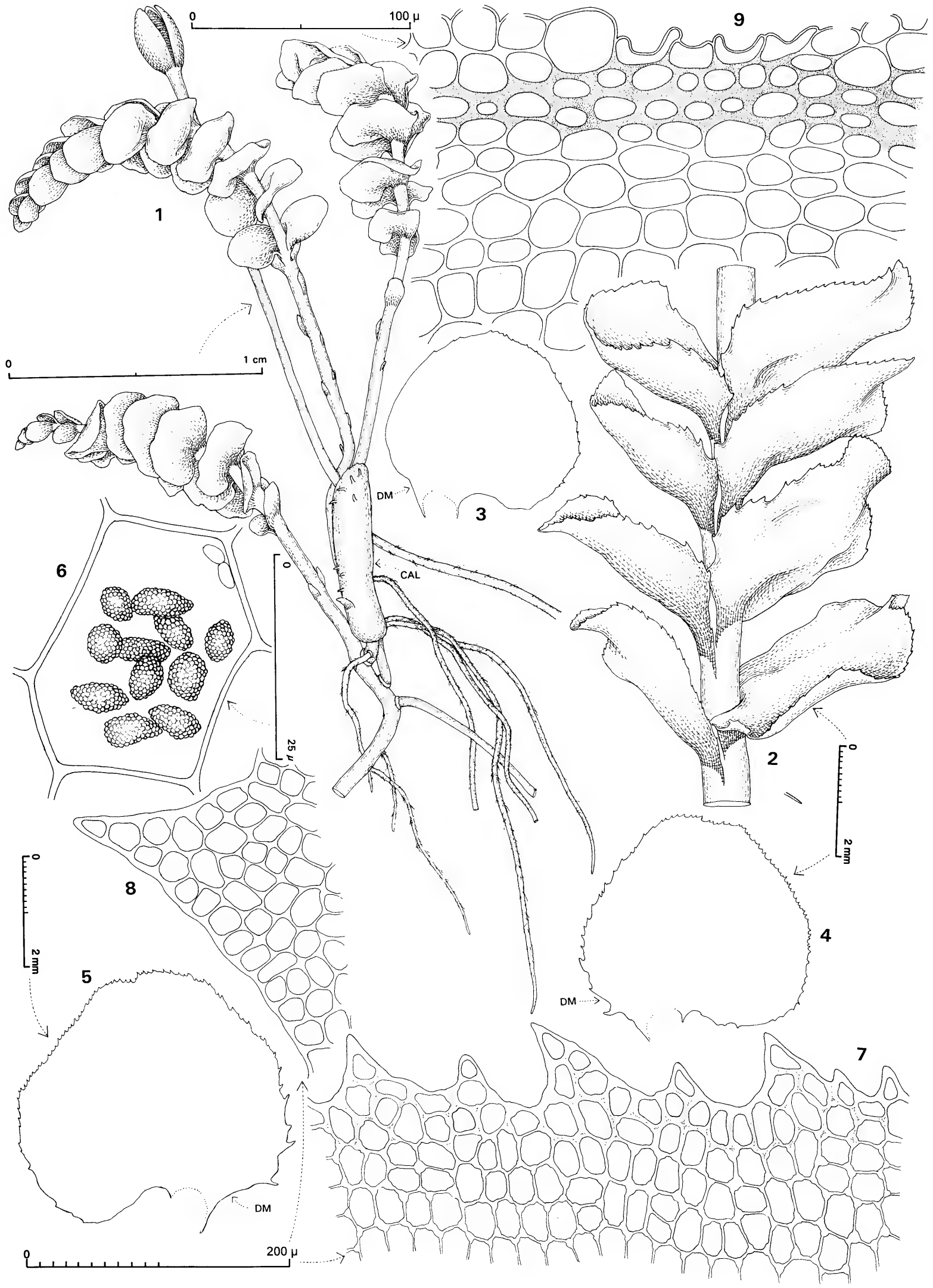

Fig. 135.
Wettsteinia schusteriana Grolle. 1. Portion of plant with mature sporophyte; note distribution of unfertilized archegonia on calyptra (= CAL). 2. Portion of main shoot, dorsal view. 3–5. Leaf outlines (DM = dorsal margin); all drawn to same scale. 6. Oil-bodies of median leaf cell. 7. Portion

appressed with opposing leaves, approximate to loosely imbricate, the insertion markedly narrow, the leaves distinctly concave, especially in dorsal, basal sector (the dorsal margin inflexed at least in the basal sector), somewhat asymmetrically orbicular to very broadly ovate to subreniform, 4200–4800 μm wide × 3600–4500 μm long, as wide as or wider than long, the dorsal and ventral bases ampliate, the ventral somewhat more strongly so and often subauriculate; margins copiously and finely dentate, the dorsal with teeth larger and more remote, the apex and ventral margin with smaller, somewhat irregular teeth. Leaves in distal sector of shoot smaller, becoming obovate. Cells in median sector of leaf with walls firm, with trigones straight-sided to weakly bulging, 22–30 μm wide × 30–40 μm long; basal cells only moderately elongated, to 50(60) μm long; marginal and intramarginal cells thick-walled. Oil-bodies hyaline, 10–18 per cell in median sector of leaf, finely papillose, the spherules very slightly protruding beyond outer membrane, the oil-bodies globose and 4.8–6.2 μm in diam. to ovoid to broadly elliptic and 4.3–5.8 × 6.7–9.1 μm, less often narrowly elliptic and 4.3 × 8.2 μm, often irregular in shape. Underleaves vestigial, in leafy sectors of shoot, especially distally, ciliiform on upper shoot sectors. Asexual reproduction absent. Fungal partner absent.

Plants dioecious. Androecia not seen. Gynoecia on strongly abbreviated intercalary branches from extreme basal, leafless sectors of upright leafy shoots; bracts and bracteoles small, bleached, irregularly laciniate, comprised of thin-walled hyaline cells. Perianth absent. Shoot-calyptra rigid, fleshy, stoutly clavate, whitish at time of capsule dehiscence, long-exserted beyond bracts, the sterile archegonia elevated on the shoot-calyptra and scattered throughout (even near the summit), the bractlets at times elevated on the shoot-calyptra, but at the time of capsule dehiscence the bractlets inconspicuous, scale-like, leptodermous, the margins irregularly crenulate-denticulate with 1-celled teeth or the bractlets falling away and the calyptra then appearing to lack them.

Seta massive, appearing ribbed (?always), with ca. 85 rows of outer rows surrounding numerous internal cells that are ± similar or a little larger. Capsule moderately long-ellipsoidal, the wall 6–8-stratose, 90–94 μm thick, the outer layer of cells equal to thickness of 2.2–3 of interior strata; outer layer of cells very small, of irregular shape, for the most part irregularly subrectangular, the walls very thin, mostly devoid of thickenings but some cells with longitudinal walls with nodular to spur-like thickenings, the cells that possess thickenings sporadic in distribution, occasionally clustered, but without a regular pattern of distribution, the transverse walls sporadically with a weak nodular swelling, the outer layer of cells near and at the capsule apex with thickenings on most walls; innermost layer of cells elongate-rectangular, the longitudinal walls with somewhat thick continuous sheets of wall material, semiannular bands on inner walls typically complete, sporadically forked.

Spores yellow-brown, 14.4–16.3 μm in diam., with low but sharply defined close papillae and very short-vermiculate markings. Elaters rather straight to somewhat tortuous, 8.6–9.6 μm wide, somewhat tapered to tips, bispiral to tips, the spirals 2.9–3.4 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (100–900 m). Known only from the eastern side of Fiordland (Lake Hauroko and Cascade Creek), Westland (all

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of median sector of ventral margin of leaf. 8. Portion of basal sector, dorsal margin of leaf. 9. Stem, cross section. (Fig. 1, from *Child 1594*, New Zealand, South Is., Lake Hauroko; 2–5, 7–9, *Engel 24697*, New Zealand, South Is., Southland EP, Waikaia State Forest, junction of Waikaia R. track and Tison Peak track; 6, from *Glenny 8917*, New Zealand, Western Nelson EP, Paparoa Ra., Moonlight Creek.)

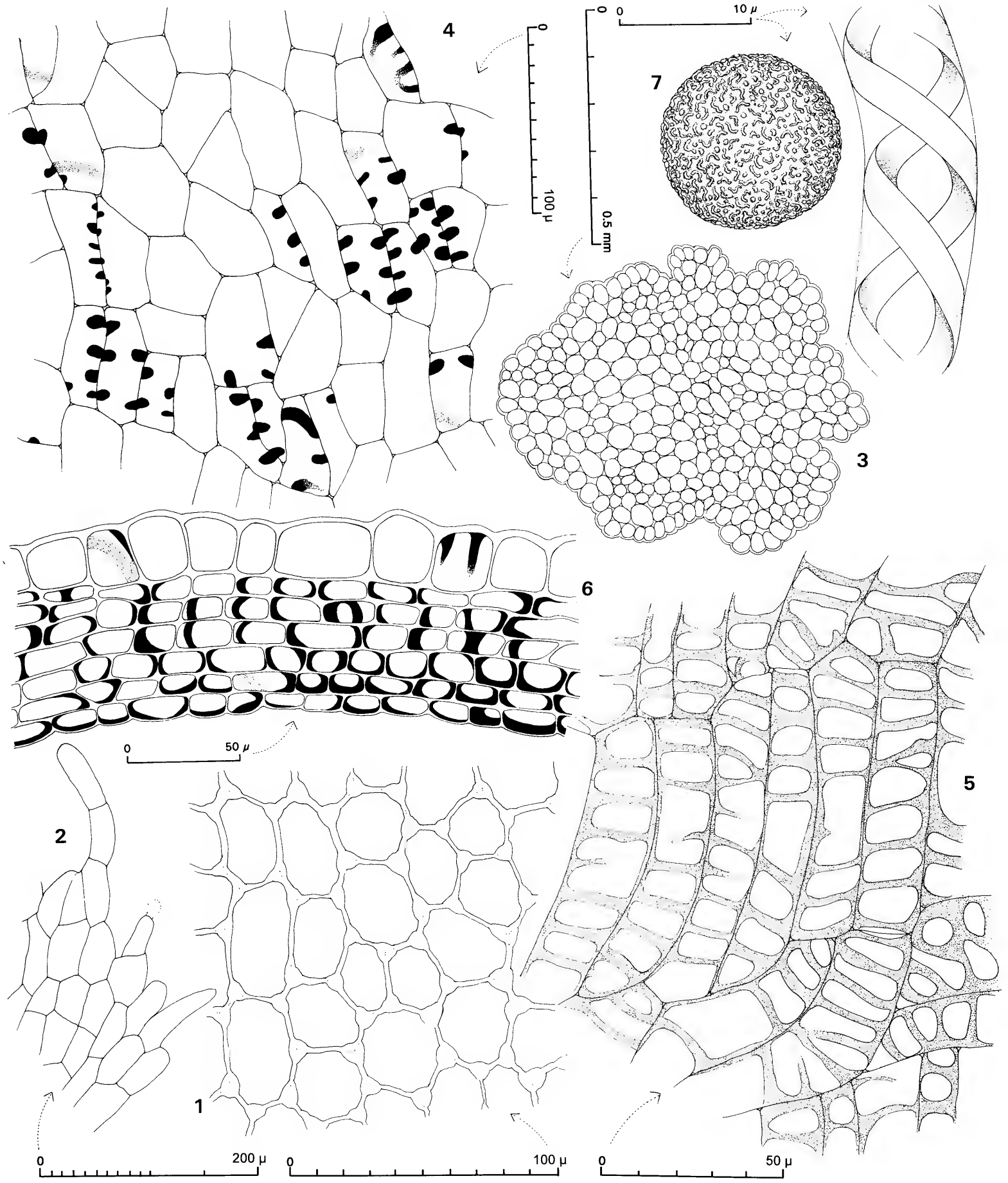

Fig. 136.
Wettsteinia schusteriana Grolle. 1. Median leaf cells. 2. Portion of lateral margin of ♀ bractlet. 3. Seta, cross section. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. 6. Capsule wall, cross section. 7. Spore and portion of elater drawn to same scale. (Fig. 1, from *Engel 24697*, New Zealand, South Is., Southland EP, Waikaia State Forest, junction of Waikaia R. track and Tison Peak track; 2, 7, *Braggins 98420*, New Zealand, South Is., Haast Pass summit; 3–6, from *Child 1594*, New Zealand, South Is., Lake Hauroko.)

records from Aspiring ER), Canterbury (Upper Bealey Valley) and Western Nelson (Moonlight Creek) EPs.

Apparently confined to *Nothofagus menziesii* and mature *N. fusca* and mixed *N. fusca* – *N. menziesii* forests. It may form large, loose, light green tufts on permanently moist, deeply shaded forest ground/humus or on bryophyte-covered logs or in vertical banks of bryophytes. At Moonlight Creek it occurs on a large *N. menziesii* trunk at a height of about 1 m. It occurs most often with *Lepidozia pendulina*, but also with *Bazzania adnexa*, *Distichophyllum crispulum*, *Plagiochila gigantea*, *Ptychomnion aciculare*, *Pyrrhobryum mnioides* and *Tylimanthus saccatus*.

Comments: This is a notable plant, distinctive by plant size, with shoots to 7 cm tall and with a strongly developed system of erect, typically unbranched leafy shoots that arise from basal, creeping, plagiotropic stolons. The erect shoots are leafless below, then gradually become larger-leaved above, but the distal sector, which is cernuous, has leaves smaller and more densely imbricate (Fig. 135: 1). The best-developed leaves on the erect shoots are in the median sector and are distinctly concave, orbicular to broadly ovate to subreniform, with the dorsal and ventral bases ampliate (Fig. 135: 2–5). The apex and margins have numerous small teeth (Fig. 135: 3–5, 7). In these respects plants are comparable to *Adelanthus*, especially *A. falcatus*. Plants of *Wettsteinia schusteriana* may be immediately distinguished, however, by the vigorous plant size and the absence of secondary pigments. The leaves of the smaller *A. falcatus* are green but stems become dark pigmented, often blackish. Also, the median leaf cells of *W. schusteriana* have small to bulging trigones and 10–18 oil-bodies per cell vs. no trigones and 4–7(10) oil-bodies per cell in *A. falcatus*. Moreover, *Wettsteinia* has a collapsing hyaloderm (Fig. 135: 9), which is lacking in all species of *Adelanthus*.

Plants of *Wettsteinia* may be confused in the field with *Tylimanthus saccatus*, which is of similar stature, is comprised of erect, typically unbranched shoots and occurs in similar habitats. Gametangial position (and type of gynoecium) will immediately distinguish these genera, but if only sterile plants are at hand. *Wettsteinia* has leaves that are very broadly ovate to subreniform and as wide as or wider than long vs. oblong in *T. saccatus*; leaf margins are finely dentate in *Wettsteinia* vs. more coarsely so in *T. saccatus*; and the stem surface is roughened in *Wettsteinia* vs. smooth in *T. saccatus*. The roughened, uneven stem surface may be seen even under the dissecting microscope, and countless air bubbles usually may be seen on the surface, likely due to the numerous partially collapsed hyaloderm cells. Also, the erect shoots in *Wettsteinia* are characteristically bent at ca. 90° about 10 mm from the apex, and the leaves become smaller toward the shoot apex (Plate 12F, Fig. 135: 1), characteristics not shared by *T. saccatus*.

Family **JACKIELLACEAE** R.M.Schust.

Jackiellaceae R.M.Schust., J. Hattori Bot. Lab. 36: 395. 1972.
Cephaloziaceae subfam. *Jackielloideae* R.M.Schust., Hepat. Anthocerotae N. Amer. 3: 649. 1974.

Plants closely creeping to prostrate, usually deep brown to fuscous, compact and firm, xeromorphic, small. Branching sparing, either exclusively ventral- or lateral-intercalary from the ventral angle of lateral leaves; stolons lacking. Stem rigid, the cortex ill-defined, a hyaloderm lacking, the cortical and medullary similar, ± firm-walled. Rhizoids freely developed, in fascicles at or near underleaf bases or from small cushions or swellings where underleaves have

been suppressed. Leaves with insertion strongly succubous, the lines of insertion not extending to stem midline dorsally, the leaves alternate, concave, ± ovate to broadly ovate-triangular to suboblate and with a rounded apex, the ventral margin dilated toward base, the leaves unlobed, the apex and margins entire. Cells strongly collenchymatous, trigones nodular to nodose-triradiate, the trigones separated by narrow, thin-walled places; surface smooth. Oil-bodies (*Jackiella curvata*) occupying conspicuous portion of cell lumen, 2(3) per cell, very pale brown, finely granular. Underleaves absent or vestigial, minute, obscure, lamella-like or consisting of 2–3 cilia, each comprised of a uniseriate row of a few cells and terminating in a slime papilla. Asexual reproduction by 2-celled gemmae.

Dioecious. Androecia on abbreviated, determinate, ventral-intercalary branches, minute, slenderly spicate; bracts in up to 25 or more pairs, small, ventricose, unlobed, the apex and margins entire; antheridia 1 per bract, the stalk short, uniseriate, the jacket-cells tiered, elongate; bracteoles absent. Gynoecia on abbreviated ventral-intercalary branches lacking normal vegetative leaves, developing a pendent, massive, rhizoidous, cylindrical marsupium, the summit with a pair of bractlets but a distinguishable bracteole lacking; perianth absent.

Sporophyte foot small, conoidal, the haustorial collar with slender, rhizoid-like, septate filaments. Seta with 8 rows of outer cells surrounding a ring of 7–8 internal cells much smaller in size and a central core of 3–4 rows of cells somewhat smaller than the subepidermal ring. Capsule long-ellipsoidal (ca. 2.3:1), the valves straight, linear, 2-stratose, the outer layer subequal to the inner layer or the inner a little thicker; outer layer of cells with one-phase development, ± tiered, short-rectangular, with strong sheet-like pigmented thickenings on all radial-longitudinal walls, the thickenings at times weakly sinuous, but nodular thickenings lacking, the transverse walls devoid of thickenings; inner layer of cells ± tiered, short-rectangular, with semiannular bands, the bands complete or, often, thin or incomplete in middle of tangential wall.

Spores minute, nearly smooth, less than elaters in diam. Elaters ± straight, rigid, bispiral.

Type: *Jackiella* Schiffn.

A family with one genus of ca. six species. The genus ranges from Indonesia to Indomalaya to Southeast Asia. *Jackiella javanica* Schiffn. ranges from New Guinea to Indonesia to Japan; *J. sinensis* (W.E.Nicholson) Grolle occurs in Yunnan, China. One species occurs in New Zealand.

Jackiella Schiffn.

Jackiella Schiffn., Denkschr. Kaiserl. Akad. Wiss., Wien Math.-Naturwiss. Kl. 70: 216. 1900. Hepat. Fl. Buitenzorg 1: 212. 1900.

Type: *Jackiella javanica* Schiffn.

The characters of the family are also those of the genus.

Reference: Schuster (2002a).

Jackiella curvata Allison & E.A.Hodgs.

[Plate 11E; Fig. 137]

Jackiella curvata Allison & E.A.Hodgs. *in* E.A.Hodgs., Trans. Roy. Soc. New Zealand 85: 571. *pl. 2, f. 11*. 1958. Holotype: New Zealand, North Is., Ngongotaha Mtn., ca. 2000 ft., Rotorua, *Allison* (MPN, Hodgson hb. no. 6386, *non vidi*).

Plants closely creeping, but when crowded in moist sites may become erect, light green in shade phases, but in exposed sites often fuscous or chocolate-brown, at times with a somewhat scorched appearance. Leaves often subvertical, dorsally assurgent, often suberect, less often obliquely spreading and then with a *Leptoscyphus*-like facies in dorsal aspect, with insertion lines not extending to stem midline dorsally, delimiting a leaf-free strip of 1–2 cells wide, the leaves imbricate, broadly ovate-triangular to suboblate, broad-based, rather ampliate at ventral base, 600–900 μm wide × 600–800 μm long, about as wide as long. Cells in median leaf large, 28–36(38) μm wide, subisodiametric, usually hexagonal, with coarse, nodose-triangular trigones, the middle lamella distinct and deep brown. Oil-bodies dull opaque, grey to very pale brown, in median cells normally 2 per cell, sporadically 3 per cell, rarely 1 per cell, at times 2–3(5) per median cell, finely granular, the spherules not protruding beyond membrane, the oil-bodies globose to narrowly to broadly elliptic, less often linear to weakly crescentic, conspicuously large, 7.8–8.8 × 10.7–13.7 μm to 8.8–10.7 × 22.4–23.4 μm.

Underleaves absent or vestigial, at times connate on one side, lamella-like to irregularly short-ciliate. Gemmae frequently present, in masses at the ± attenuate shoot tips, brownish green to reddish brown, ellipsoidal, 2-celled, 13–17 × 20–25 μm.

Sporophyte as in family description.

Distribution and Ecology: New Zealand: South Island (ca. 100–200 m), North Island (365–650 m); Australia: Tasmania, Victoria. Known in New Zealand from Westland, Southern North Island, Volcanic Plateau, Auckland and Northland EPs.

In the South Island known only from scattered sites. It occurs, for example, near Hercules Creek (Mt. Hercules Scenic Reserve, south Westland, ca. 100 m) and on road banks above the Tiropahi River (north Westland, 200 m). It is widespread in the North Island (and often abundant northward), commonly in disturbed sites, such as exposed soil of roadside banks and soil between rocks in road cuts. The species grows on compact mineral soils and occurs in thin, at times rather large, mats or as scattered small patches. Also on vertical clayey banks, at times associated with *Blechnum*, or over exposed, soil-covered rock walls such as in scrub forests of *Leptospermum scoparium*, *Weinmannia silvicola* and *Dacrydium cupressinum* (ridge between Webb Creek Track and Billy Goat Track, Coromandel Forest Park). These are warm, sunny sites, often without other accompanying hepatics, and in these niches plants are able to tolerate desiccation; in exposed sites plants are typically fuscous or chocolate-brown. The species occasionally grows on well-shaded banks, and in such cases plants are light green. In more mesic sites, sometimes associated with *Isotachis*, chiefly *I. lyallii*, but also *I. montana*, *Baeomyces heteromorphus*, *Campylopodium medium*, *Ditrichum difficile*, *Lycopodium scariosum*, *Polytrichadelphus magellanicus*, *Riccardia crassa* and *Stereocaulon ramulosum*. One collection was made from the base of a *Leptospermum scoparium* trunk, where the *Jackiella* was growing with *Cuspidatula monodon*, *Frullania aterrima*, *Hypnum cupressiforme*, *Macromitrium gracile* and *Thuidium furfurosum*.

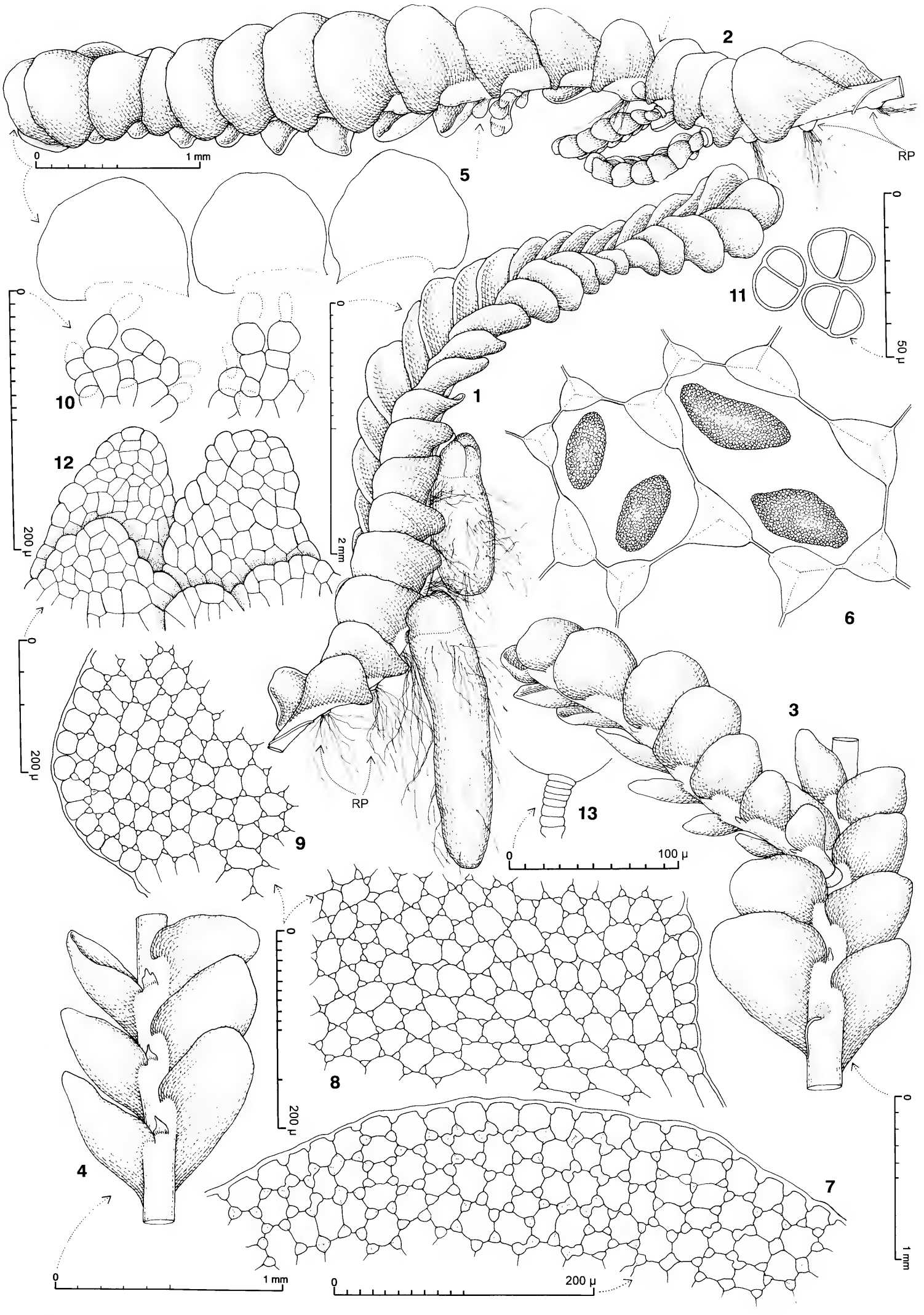

Fig. 137.
Jackiella curvata Allison & E.A.Hodgs. 1. Leading shoot with mature and submature marsupia; note bractlets at mouth of both marsupia (lateral view) and convex rhizoid pads (= RP) visible near shoot base. 2. Main shoot (lateral view) with 2 mature ventral-intercalary androecial branches; note accessory scale-like lamellae at arrows and rhizoid pads (= RP). 3. Portion of leading shoot with

Comments: See under the genus. Among the few closely creeping hepatics in New Zealand with strongly succubous, unlobed leaves (Fig. 137: 2), *Jackiella curvata* may be confused only with some *Solenostoma* species, which are comparable in aspect and size and which may occur on similar (but usually more mesic) roadside habitats and banks. Moreover, the collenchymatous cells each with 2–3 large oil-bodies (Fig. 137: 6) also may occur in *Solenostoma*. However, the chocolate-brown to deep brown color of the plants, without a trace of reddish pigmentation typical of *Solenostoma*, will immediately separate *J. curvata* from any other regional taxon. *Jackiella* is immediately distinct in rhizoid position: only in fascicles from the bases of vestigial underleaves (Fig. 137: 2) or, if rhizoids are absent, rounded convexities or small cushions that represent rhizoid-initials may be distinguishable. Also, branching in *Jackiella* is purely intercalary (Fig. 137: 3).

Suborder 8. **JUNGERMANNIINEAE** R.M.Schust.

Jungermanniales suborder *Jungermanniineae* R.M.Schust.

Family **JUNGERMANNIACEAE** Rchb.

Jungermanniaceae Rchb., Botanik für Damen, Künstler und Freunde ... 256, Tab. zu p. 248. 1828 (1827).

Jamesoniellaceae He-Nygrén, Juslén, Ahonen, Glenny & Piippo in He-Nygrén et al., Cladistics 22: 27. 2006.

Plants anisophyllous, usually procumbent or creeping, more rarely erect, opaque, chlorophyllose, and mostly forming red, vinaceous and/or brown wall pigments, medium to large and robust. Branching irregular, sparing, the branches for the most part of *Frullania* type and lateral-intercalary type (the intercalary branches dorsally displaced in *Andrewsianthus*, often ventrally displaced); ventral-intercalary branches in a few species; *Radula*-type basiscopic branches in some taxa; stolons present in some species, geotropic. Stems with cortex weakly differentiated, not forming a hyaloderm. Rhizoids scattered on ventral surface of the stem, rarely more frequent near the ventral leaf base, rarely (*Notoscyphoideae*) on underleaf bases. Leaves with insertion varying from nearly transverse (but with ventral half usually succubous) to strongly succubous, extending to the stem midline dorsally (beyond in *Gottschelia* and some *Jamesonielloideae*; a leaf-free strip present only in *Vanaea*), with apices undivided or bilobed, less often 3–4-lobed; margins entire (except *Chandonanthus*) or sometimes armed at bases. Cells usually with trigones small to bulging, at times firm-walled; surface often striate-papillose. Oil-bodies usually coarsely granular to papillose, rarely homogeneous. Underleaves

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ventral-intercalary branch, and, near leaf scar at base, a rhizoid pad; ventral view. 4. Sector of shoot showing rudimentary underleaves, ventral view. 5. Leaves. 6. Cells with oil-bodies (× 733). 7. Distal sector of leaf. 8. Dorsal base of leaf. 9. Ventral base of leaf. 10. Underleaves. 11. Gemmae. 12. Bractlets from mouth of marsupium. 13. Antheridial stalk. (Figs. 1–5, 7–13, from *Engel 6562*, New Zealand, South Is., Westland EP, Mt. Hercules Scenic Reserve; 6, from *Engel 22353*, New Zealand, North Is., Auckland EP, Coromandel Forest Park, ridge between Webb Creek Track and Billy Goat Track.)

either absent or small, rarely to 0.4× leaves in size (larger in *Pseudocephaloziella*), lanceolate (bilobed in *Notoscyphus*). Asexual reproduction, if present, by gemmae.

Dioecious or paroecious, rarely autoecious. Androecia on leading shoots, terminal but becoming intercalary; antheridia 1–3 per bract, the stalk 1–2-seriate. Gynoecia on leading shoots; bracteole to 0.6× bract area, often connate with bracts on one or both sides, or vestigial or absent. Perianth normally present, varying from long and long-emergent (then normally lacking a subtending *Isotachis*-type perigynium or low marsupium) to abbreviated and ± included within the bracts (then the perianth is normally subtended by a well-developed stem perigynium); perianth usually variously plicate (at least near the mouth), occasionally eplicate, the mouth usually contracted.

Seta usually of numerous cells (reduced in *Gerhildiella*). Capsule ovoid to short-ellipsoidal, the wall 2–4(7)-stratose; outer layer of cells with nodular thickenings; inner layer of cells with semiannular bands.

Spores papillose-short-vermiculate to verrucate (coarsely and irregularly warty) or baculate. Spore:elater diam. ratio usually ca. 2:1 (ca. 4:1 in *Andrewsianthus*). Elaters bispiral.

Type: *Jungermannia* L.

A diverse, polytypic family with eight subfamilies, outlined as follows; note that many of the genera are monotypic.

1) subfam. *Chandonanthoideae* Inoue has three genera: *Chandonanthus* Mitt., monotypic, which occurs in temperate Australasia; extra-Austral genera are *Plicanthus* R.M.Schust. (5 species) and *Tetralophozia* (R.M.Schust.) Schljakov (3–4 species);

2) subfam. *Lophozioideae* Macvicar has 12 genera; the Austral genera include:

   a) *Anastrophyllum* (Spruce) Steph., which is widespread in south temperate areas (Engel and Braggins [1998] treat the south temperate species);

   b) *Andrewsianthus* R.M.Schust., with several species in south temperate areas;

   c) *Gymnocoleopsis* (R.M.Schust.) R.M.Schust. has three species, one, *G. cylindriformis* (Mitt.) R.M.Schust., occurs on Kerguelen Island and Prince Edward Island; a second, *G. capensis* (S.W.Arnell) R.M.Schust., is from South Africa; a third species, *G. multiflorus* (Steph.) R.M.Schust., is montane/alpine in the northern Andes and tropical Africa;

   d) *Lophozia* (Dumort.) Dumort. is widespread in south temperate and subantarctic areas;

   e) *Roivainenia* Perss. (cf. Persson and Grolle, 1961) is monotypic and occurs on South Shetland Islands (Bednarek-Ochyra et al., 2000), South Georgia, Falkland Islands (Engel, 1990a) and southern South America (Magellanian and Valdivian regions; see range in Engel, 1990a);

   f) *Sphenolobopsis* R.M.Schust. & N.Kitag., with *S. pearsonii* (Spruce) R.M.Schust. & N.Kitag., occurs in oceanic western Europe, southern Appalachians, NW North America and on Tristan da Cunha (*S. kitagawae* R.M.Schust. occurs in Borneo and New Guinea).

   Extra-Austral genera are *Anastrepta* (Lindenb.) Schiffn. (monotypic); *Gerhildiella* Grolle (monotypic); *Gymnocolea* (Dumort.) Dumort., with a few species; *Hattoria* R.M.Schust. (monotypic); *Pseudocephaloziella* R.M.Schust. (monotypic); and *Sphenolobus* (Lindb.) Berggr.

3) subfam. *Jungermannioideae* has 11 genera, four of them Austral:

a) *Arctoscyphus* Hässel, with two species, both from southern South America (cf. Hässel, 1990; Schuster, 2002a);

b) *Cryptostipula* R.M.Schust., monotypic, of New Zealand (the status of this genus is uncertain and will be evaluated and discussed in volume 2 of this series);

c) *Invisocaulis* R.M.Schust., monotypic and known only from Prince Edward Island (Schuster, 2002a);

d) *Solenostoma* Mitt., with several species in southern temperate areas.

Extra-Austral genera are *Cryptocolea* R.M.Schust. (monotypic); *Cryptocoleopsis* Amakawa (monotypic); *Diplocolea* Amakawa (monotypic); *Horikawaella* S.Hatt. & Amakawa (monotypic); *Jungermannia* L. (*s. str.*, with 7–8 species); *Nardia* Gray; and *Phragmatocolea* Grolle (monotypic).

4) subfam. *Jamesoniellioideae* Inoue has eight genera; the Austral ones are:

a) *Cryptochila* R.M.Schust., with several species in south temperate areas;

b) *Cuspidatula* Steph. has two species, one in our area;

c) *Jamesoniella* (Spruce) Carrington has several species in south temperate areas;

d) *Nothostrepta* R.M.Schust. has two species, *N. bifida* (Steph.) R.M.Schust. of the Falkland Islands, southern South America and Juan Fernandez, and *N. longissima* (Steph.) R.M.Schust. of southern South America (Engel, 1978, 1990a; Schuster, 1980c, 2002a);

e) *Pisanoa* Hässel, monotypic, of southern South America (between 51° and 52° S in wet, coastal southern Chile) (Hässel, 1989; Schuster, 2002a).

Extra-Austral genera are *Anomacaulis* (R.M.Schust.) R.M.Schust. (monotypic); *Denotarisia* Grolle (monotypic); and *Vanaea* (Inoue & Gradst.) Inoue & Gradst. (monotypic). Inoue (1966) included *Syzygiella* and *Syzygiella* subg. *Protosyzygiella* in the *Jamesonielloideae*. Schuster (1980b, p. 334) elevated the last to generic rank and included both in subfam. *Syzygielloideae* R.M.Schust., of the *Plagiochilaceae*. Schuster (2002a, p. 402) included *Syzygiella* and *Protosyzygiella* in a key to the genera of the *Jamesonielloideae*, but stated (p. 402) "although Inoue placed these genera in Jamesonielloideae I think a closer affinity is to the Plagiochilaceae ..." Recent molecular analyses (e.g., Hentschel et al., 2006; He-Nygrén et al., 2006) demonstrated that the affinities of these genera are not with members of *Plagiochilaceae*, but rather their phylogenetic affinities lie elsewhere. Until further molecular studies are done on these genera, we follow Inoue (1966) in placement of these taxa in subg. *Jamesonielloideae*. *Protosyzygiella* (Inoue) R.M.Schust. has one species, *P. pseudoconnexa* (Herzog) R.M.Schust., of southern South America. *Syzygiella* has ca. 20 species, and is mostly Neotropical.

5) subfam. *Gottschelioideae* R.M.Schust. has one genus, *Gottschelia* Grolle, with two species, and is extra-Austral.

6) subfam. *Scaphophyloideae* R.M.Schust. has one genus, *Scaphophyllum* Inoue, monotypic, and is extra-Austral.

7) subfam. *Notoscyphoideae* R.M.Schust. has one genus, *Notoscyphus* Mitt., with two species; *N. belangerianus* (Lehm. & Lindenb.) Mitt. occurs in Cape Prov., South Africa.

8) subfam. *Eremonotoideae* R.M.Schust. has two genera, both monotypic and extra-Austral, *Eremonotus* Lindb. & Kaal. *ex* Pearson and *Paramomitrion* R.M.Schust.

Rhodoplagiochila R.M.Schust. has only *R. rosea* R.M.Schust. of Venezuela (Estado Merida, Sierra de Santo Domingo, 3700–3750 m) and was placed by Schuster (1978, 1980b) in *Plagiochilaceae*. Inoue (1984) placed the genus in "Lophoziaceae," and Gradstein et al. (2001) followed with a placement in *Jungermanniaceae*. The genus remains poorly known and subfamilial placement has not been made.

Bragginsella R.M.Schust., a monotypic genus of New Zealand, was placed by Schuster (1997a) in subfam. *Jungermannioideae*, but, based on the discovery of fertile material, was assigned by Glenny and Malcolm (2005) to *Geocalycaceae* (see volume 2 of this series for further discussion).

Subfam. ***Chandonanthoideae*** Inoue

Subfamily *Chandonanthoideae* Inoue, J. Hattori Bot. Lab. 29: 178. 1966.

Chandonanthus Mitt.

Chandonanthus Mitt. *in* Hook.f., Handb. N. Zeal. Fl. 750, 753. 1867.

Plants strongly anisophyllous, erect (when terricolous or saxicolous) to pendulous (when epiphytic), yellowish or golden brown, at times reddish brown, vigorous, often 10–20 cm long or more, to 3 mm wide or more. Branching sparingly, the branches typically of *Frullania* type; half-leaf broadly ovate; first branch underleaf large, asymmetrically bifid + laciniate near base. Stems with paraphyllia present, conspicuous, of diverse form, filiform to lanceolate. Stems rigid, cortex rigid, of 4–5 layers of very thick-walled cells with reduced lumina; medullary cells larger, firm-walled, hyaline. Rhizoids typically present only toward base of leafy shoots, lacking above. Leaves widely spreading, often dorsally assurgent, imbricate, broadly quadrate-ovate, the lamina plicate and undulate, the margins entire except, often, with a few to several cilia or laciniae at the dorsal and ventral bases, (1200)1500–2300 μm wide × (900)1300–1800 μm long, bilobed to ca. 0.5; lobes often abaxially sulcate, broadly acute and with arched margins, at times subapiculate, the tips markedly sharp. Cells with trigones coarse, strongly nodose, often confluent, the cell lumina surrounded mostly by trigones which are separated by narrow, thin-walled places; cells of leaf base longer, the longitudinal walls often each with 1–3 conspicuous nodose intermediate thickenings; surface densely covered with hemispherical, variably sized papillae. Oil-bodies occupying a small volume of cell, hyaline, opaque, dull greyish, (4)5–7 per cell in median sector of lamina, 2–4 per cell toward lobe base, minutely and finely but distinctly granular or moderately papillose, globose to broadly elliptic (often irregularly so), 4.3–6.2 × 2.9–4.3 μm, spherical ones 3.4–4.3 μm in diam. Underleaves large, subquadrate, bifid to ca. 0.55–0.65, the lobes protracted and ciliiform distally, the margins with several cilia/laciniae; lamina margins with several variable cilia/laciniae. Asexual reproduction absent.

Dioecious. Androecia becoming intercalary on leading shoots or elongate *Frullania*-type branches, subfolious, the bracts similar to vegetative leaves in size, orientation and shape except for basal portion of dorsal lobe which is deeply ventricose, the saccate portions of opposing bracts closely juxtaposed, the bracts rather tightly appressed to bract immediately above; margin of ventral lobe similar to that of leaves; androecia with stem paraphyllia similar to those of sterile portions of shoot, the lobule large for bract size, with margins sharply inflexed to involute to form a pouch, the margin with an acuminate projection, but otherwise with a few sometimes stalked slime papillae; antheridia 2–3 per bract, the stalk 23–26 cells long, biseriate, the jacket-cells scattered; bracteoles large, like underleaves, without antheridia. Gy-

noecial bracts of innermost series bifid to 0.5–0.65, the apices long-acuminate and becoming ciliiform, the margins ciliate to laciniate; bracteole similar, subequal to bracts or ca. 0.55–0.65 the bract size; paraphyllia copiously developed on the abaxial bases of bracts and bracteole as well as in their axils. Perianth large, ellipsoidal, deeply 6–8-plicate for 0.75–0.9 its length, the mouth with numerous laciniiform-caudate, narrow lobes that may bear 1–2 lateral cilia.

Seta massive. Capsule dehiscing to base into 4–6 valves, the wall fleshy, 90–120 μm thick, of 6–8 layers, the outer layer equal to thickness of 2.3–3 of interior strata; outer layer of cells small, never tiered, subquadrate to short-subrectangular, with one-phase development (the outer layer at times with a two-phase ontogeny at most moderately developed), the radial walls slightly thickened, with red-brown short to often somewhat elongate nodule-like thickenings on longitudinal walls, the transverse walls with thickenings fewer or absent, the outer layer with sporadic semiannular bands; exposed tangential wall in surface view covered with a hyaline, amorphous substance, sometimes wrinkled in appearance, sometimes organized into sharp, conical thickenings lying ± parallel to surface, the substance nearly obliterating detail of nodular thickenings of outer layer; intermediate layers of cells subequal in thickness, with thickenings often feebly tangentially dilated, semiannular bands absent; innermost layer of cells mostly irregularly long-rectangular, the radial walls with moderately thick continuous sheets of red-brown wall material, with semiannular bands, the bands red-brown, common, wide, rather widely spaced, mostly complete, sporadically forked.

Spores 25.4–28.8 μm in diam., red-brown, with coarse, rather close but not crowded papillae and sometimes short-vermiculate ridges. Elaters tortuous, 9.6–13 μm wide, bispiral, the spirals 2.9–3.8 μm wide, loosely wound.

Type: *Chandonanthus squarrosus* (Hook.) Mitt. *ex* Schiffn. (≡ *Jungermannia squarrosa* Hook.)

A genus accepted here in the narrow sense, with only one species, which is known only from New Zealand, Tasmania and southeast Australia. The genus was formerly recognized in a broader sense that included *Chandonanthus* subg. *Tetralophozia*, which was raised to the generic rank by Schljakov (1976). *Tetralophozia* (R.M.Schust.) Schljakov has four species and is treated in Schuster (2002b).

Reference: Schuster (2002b).

Chandonanthus squarrosus (Hook.) Mitt. *ex* Schiffn.

[Plate 13E; Figs. 138, 139]

Jungermannia squarrosa Hook., Musci Exot. 1: *t. 78*. 1818. *Chandonanthus squarrosus* (Hook.) Mitt. *ex* Schiffn., Engl. & Prantl, Nat. Pflanzenfam. 1(3), 1: 106. 1895. Type: New Zealand, Dusky Bay, *Menzies*.

Anastrophyllum tasmanicum Rodway, Pap. & Proc. Roy. Soc. Tasmania 1916: 46. 11 July 1916 (Tasman. Bryoph. 2: 37. 30 Aug. 1916) ≡ *Roivainenia tasmanica* (Rodway) Grolle, J. Jap. Bot. 41: 146. 1966. Lectotype (*fide* Engel and Braggins, 1998): Tasmania, Mt. Hartz Plateau, Dec. 1914, *Rodway – c. per.* (HO!).

Acrobolbus aequaelobus E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 81. 1965. Holotype: New Zealand, Maungawaru Plateau, Raukumara Ra., Jan. 1953, *Druce* (MPN, *non vidi*); isotype: (CHR!).

For description see the genus.

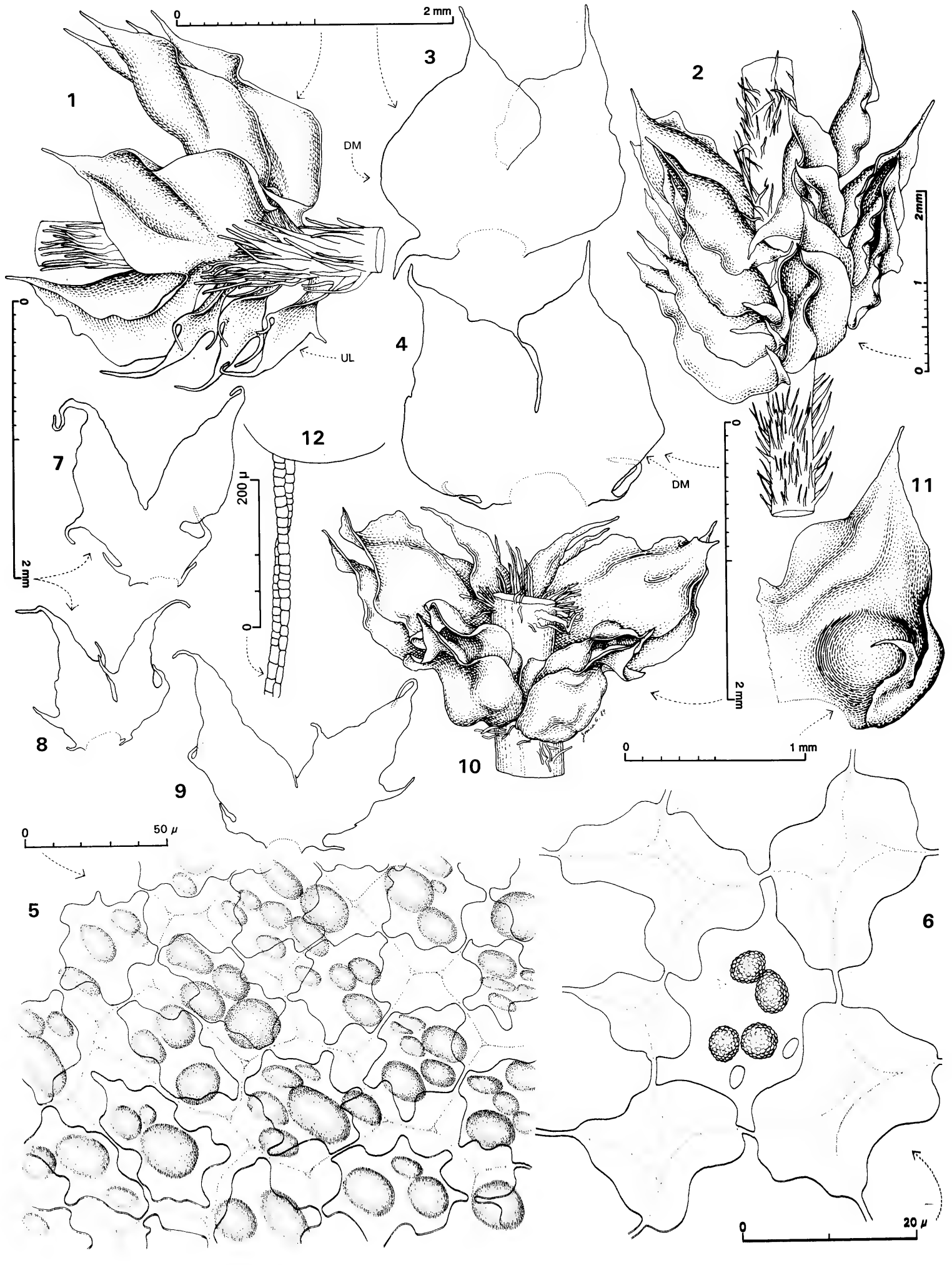

Fig. 138.
Chandonanthus squarrosus (Hook.) Mitt. *ex* Schiffn. 1. Portion of shoot, lateral view, showing 2 leaves on far side of axis, 1 on near side and 3 underleaves (= UL); note stem paraphyllia. 2. Portion of shoot with some leaves removed to show stem paraphyllia, dorsal view; note stem paraphyllia. 3, 4. Leaf outlines (flattened) (DM = dorsal margin). 5. Cells of lower sector of leaf lobe showing large surface papillae. 6. Median cells with oil-bodies. 7–9. Underleaves, all drawn to same scale. 10. Sector of androecium showing 2 pairs of bracts, dorsal view. 11. Dorsal lobe of ♂

Distribution and Ecology: New Zealand: Auckland Islands (150–360 m), Antipodes Islands (145–300 m), Stewart Island, South Island (70–1530 m), North Island (240–1370 m); Australia: Tasmania, Victoria. Known in New Zealand from Fiordland, Southland (Garvie Mtns., Ajax Hill swamp), Otago (coastal and inland), Canterbury (including Banks Peninsula), Westland, Western Nelson, Sounds–Nelson, Marlborough (Mt. Stokes, Hodder River), Southern North Island, Taranaki, Volcanic Plateau, Gisborne, Auckland and Northland EPs.

A species with a notably broad ecological amplitude, especially with regard to habitat-moisture availability and exposure. It may form mound-like, pure, often huge, dense, thick clumps or masses on the forest floor, often in well-drained conditions such as steep slopes. Also present over rock and boulders, at times where some soil has accumulated, as well as on cliff faces and exposed rocky knolls. It is able to tolerate considerable exposure, e.g., it forms large, pure patches on soil over rock of an old lava flow on Rangitoto Island (Auckland) and in such exposed situations often is associated with the moss *Racomitrium*. In such terrestrial habitats it is found with *Anastrophyllum schismoides*, *Bazzania involuta* var. *submutica*, *Dicranoloma billardierei*, *Distichophyllum pulchellum*, *Gackstroemia alpina*, *G. weindorferi*, *Hypnum chrysogaster*, *Jamesoniella colorata*, *Leifidium tenerum*, *Leptotheca gaudichaudii*, *Racomitrium crispulum*, *R. pruinosum* and *Wijkia extenuata*. At times as small tufts on shrubs or as mounds "capping" tree stumps, or on tree trunks (e.g., of *Nothofagus*), at times occupying large areas of the trunk. In forests it is a common upper branch epiphyte (on *Dacrydium cupressinum*, *Dracophyllum longifolium*, *D. traversii*, *Halocarpus biformis*, *Leptospermum scoparium*, *Nothofagus fusca*, *N. menziesii*, *N. solandri*, *Olearia colensoi*, *Podocarpus totara* and *Weinmannia racemosa*) and appears to be a tree-canopy species. It is not uncommon on fallen tree branches of various sizes, often in large masses. Such masses are particularly noteworthy for the size and density: on the track to Alex Knob (Westland Natl. Park, 900 m) a mass over 1 kg in weight and ca. 60 cm in diam. was observed fallen on the floor. Hepatics in tree-canopy niches must, to some degree, be drought-tolerant since during rain-free periods the habitat is xerophytic except for mists and fog. The species also is common on tree trunks and branches at the forest edge and in low forest near the treeline. As an epiphyte it is found with *Cuspidatula monodon*, *Dicnemon calycinum*, *D. semicryptum*, *Lepicolea attenuata*, *Lepidolaena taylorii*, *Leptostomum inclinans*, *Macromitrium longipes*, *Plagiochila circinalis* and *Weymouthia mollis*.

Comments: A distinctive plant, especially when well developed, that should not be confused with any other of our species. Plants are vigorous and the shoots simple or sparingly branched. Shoots have a curious 4-angled appearance due to the 4 regular rows of leaf apices, with each leaf bifid (Fig. 138: 1, 2). Underleaves are large, also bifid, with lobe and lamina margins with several variable cilia/laciniae (Fig. 138: 7–9). The stems are densely paraphyllose (Fig. 138: 1, 2), a condition that may be easily seen with a hand lens.

Suboptimal plants may offer confusion. For example, plants on small branches of *Olearia* growing prostrate over a mat of *Frullania aterrima* are small for the species and have dorsally assurgent leaves with lobes that are plane and not canaliculate. Such plants have a superficial resemblance to a *Lophozia*. Such plants, however, have characters of *Chandonanthus*

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bract. 12. Antheridium. (Figs. 1–4, 7–9, from *Engel 13771*, Tasmania, near Scotts Peak Road; 5, from New Zealand, South Is., Westland EP, Westland Natl. Park, Franz Josef Glacier Valley; 6, from *Glenny 8921*, New Zealand, South Is., Canterbury EP, Arthur's Pass, Margaret Tarns track; 10, 11, from *Engel 16711*, Tasmania, Clear Hill Road; 12, from *Engel 13645*, Tasmania, Adamsfield Track.)

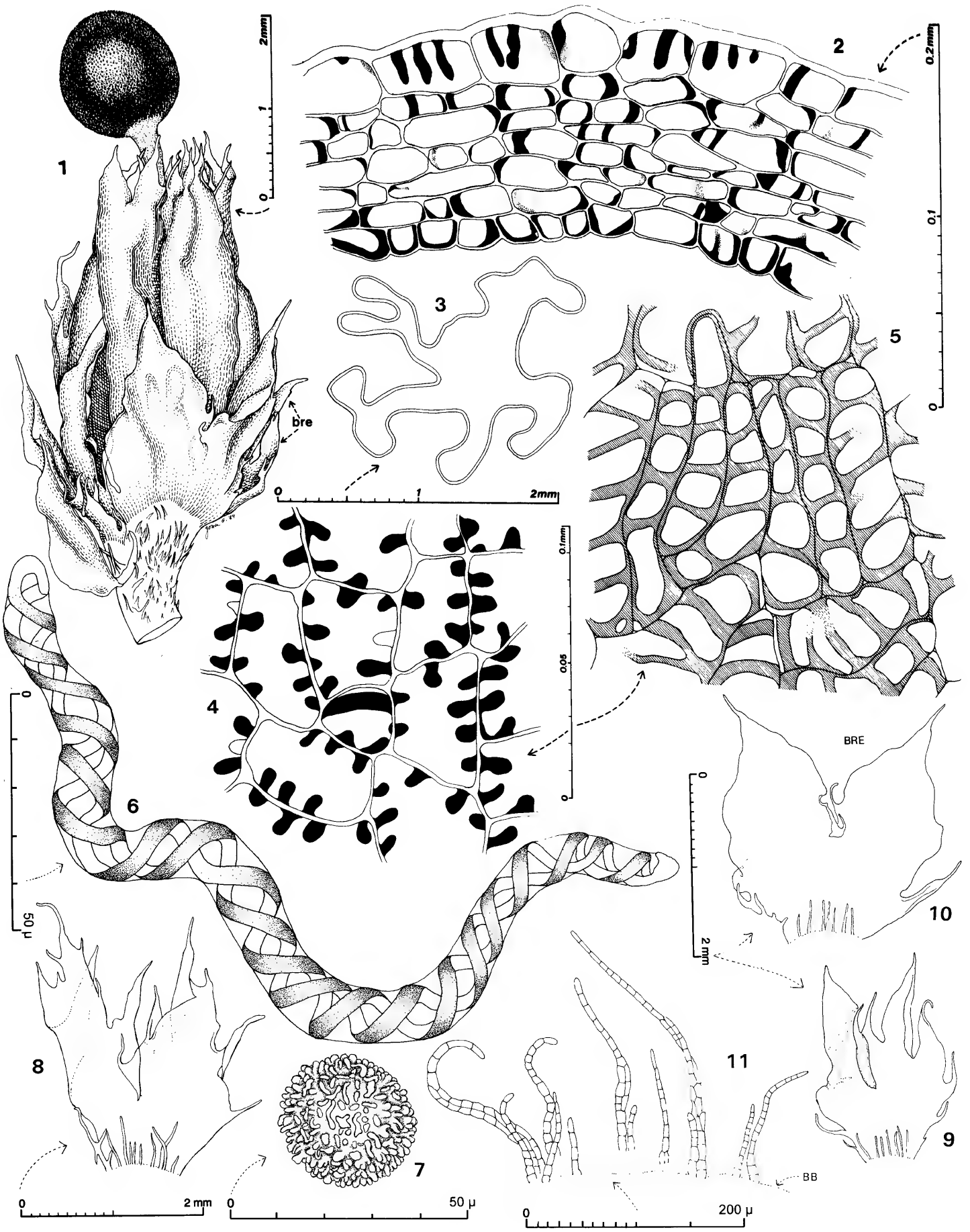

Fig. 139.
Chandonanthus squarrosus (Hook.) Mitt. 1. Gynoecium with mature sporophyte, dorsal-lateral view (the 2 lower bracts on right side removed); note the accessory lobes on bracts (bre = bracteole). 2. Capsule wall, cross section. 3. Perianth, cross section through median portion. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. 6. Elater. 7. Spore. 8–10. Bracts and bracteole (= BRE) from same innermost series, abaxial view; note fringe of paraphyllia at bases. 11. Paraphyllia on abaxial surface of base of innermost bract (BB = bract base). (Figs. 1, 6–11, from *Engel 13771*, Tasmania, Near Scotts Peak Road, E of S end of Lake Gordon; 2, 4, 5, from *Engel 15119*, Tasmania, Sentinel Ra., between Lakes Gordon and Pedder; 3, from *Engel 14305*, Tasmania, Cradle Mtn.–Lake St. Clair Natl. Park.)

squarrosus such as a) presence of distinct underleaves, though small for the shoot size compared to well-developed plants; b) stem paraphyllia, though smaller in stature and more sparsely developed; and c) well-developed surface papillae that are very similar to those of well-developed plants.

Subfam. ***Lophozioideae*** Macvicar

Subfamily *Lophozioideae* Macvicar, Stud. Handb. Br. Hepat. ed. 1, 593. 1912.

Lophozia (Dumort.) Dumort.

Lophozia (Dumort.) Dumort., Recueil Observ. Jungerm. 17. 1835. *Jungermannia* sect. *Lophozia* Dumort., Syll. Jungerm. Europ. 53. 1831.

Isopaches Buch, Mem. Soc. Fauna Fl. Fennica 8: 287. 1932.

Leiocolea (Müll.Frib.) Buch, Mem. Soc. Fauna Fl. Fennica 8: 288. 1932. *Leiocolea* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland, ed. 2, 6(1): 711. 1920.

Obtusifolium S.W.Arnell, Illus. Moss Fl. Fennoscandia 1 (Hep.): 133, 309. 1956.

Massula Müll.Frib. *ex* Schljakov, Novit. Syst. Plant. Non Vasc. 9: 314. 1972, *nom. illeg.* (*non* Dulac, 1867, *Typhaceae*). *Lophozia* subg. *Massula* Müll.Frib., Ber. Deutsch. Bot. Ges. 57: 341. 1939, *nom. inval.*

Protolophozia (R.M.Schust.) Schljakov, Novit. Syst. Plant. Non Vasc. 16: 204. 1979. *Lophozia* subg. *Protolophozia* R.M.Schust., Nova Hedwigia 15: 472. 1968.

Plants anisophyllous, usually prostrate, at times ascending to suberect, pale to pure green but often tinged with reddish to vinaceous or brownish pigments, variable in size, from tiny and under 500 μm wide to vigorous and 2.5–5 mm wide, the shoot apices not becoming flagelliform. Branching variable, *Frullania*-type and ventral- and lateral-intercalary type branches present in various species and combinations; basiscopic-terminal (*Radula*-type) branches occasional; geotropic stoloniform branches absent (except subg. *Hypolophozia*). Leaves succubously inserted and oriented, concave to ± canaliculate, 2-, 3-, or 4-lobed, if 3-lobed, the dorsal lobe largest; lamina margins usually entire, at times with a few teeth, especially toward the base. Cells thin-walled and lacking trigones in some taxa but trigones mostly present; surface striate-papillose or smooth. Oil-bodies usually granular, occasionally homogeneous. Underleaves varying from bifid to undivided and lanceolate (then usually with 1 to several cilia or laciniae each terminating in a slime papilla) to vestigial or lacking. Gemmae often present, green, brownish or reddish, usually 1–2-celled, smooth or angulate.

Autoecious, paroecious or dioecious. Gynoecial bracts larger than leaves, usually sheathing the perianth base, 2–3–4-lobed; bracteole usually distinct, large, free or broadly connate with bract on one side and at times narrowly so on the other. Perianth long-emergent, cylindrical or ovoid or clavate, usually plicate in distal 0.2–0.5.

Seta usually massive and of general type, in minute taxa sometimes with 8–10 outer + 4 or more inner cell rows. Capsule wall (2)3–5 stratose; outer layer of cells usually at most slightly elongated, with all longitudinal walls and most longer transverse ones with nodular thickenings; inner layer of cells usually with distinct semiannular bands.

Type: *Lophozia ventricosa* (Dicks.) Dumort. (≡ *Jungermannia ventricosa* Dicks.)

A large (65–70 species), complex and often difficult genus with a cosmopolitan distribution. The greatest number of species are found in the boreal to subarctic regions of the Northern Hemisphere (43 species of *Lophozia* and *Barbilophozia* are listed for North America in

Stotler and Crandall-Stotler [1977]; these are treated in detail in Schuster [1969c]). The genus has some species occurring in the south temperate zone, but it is not "species rich in cool/cold Austral regions" as stated by Schuster (2002a, p. 232). Chile has eight species and New Zealand has 10 species; these and other southern temperate and subantarctic species belong to a number of diverse subgenera, as follows.

1) subg. *Orthocaulis* (Buch) R.M.Schust. has two Austral species: *L. anomala* R.M.Schust. (= *Orthocaulis longiflorus* Herzog, Rev. Bryol. Lichénol. 23: 32. 1954, *non Lophozia longiflora* Nees) from southern Chile and *L. leucorhiza* (Mitt.) R.M.Schust. from Kerguelen Island.

2) subg. *Barbilophozia* (Loeske) Müll.Frib., with *L. hatcheri* (A.Evans) Steph., is bipolar, in the Southern Hemisphere occurring on the southernmost tip of South America, Falkland Islands (Engel, 1990a) and in the maritime Antarctic (Bednarek-Ochyra et al., 2000).

3) subg. *Protolophozia* R.M.Schust. has the most Austral representatives. *Lophozia crispata* R.M.Schust. and *L. gymnocoleopsis* R.M.Schust. & J.J.Engel occur in southern South America; *L. androgyna* R.M.Schust. and *L. tasmanica* R.M.Schust. are both from Tasmania; and *L. lancistipa* (Grolle) R.M.Schust. occurs on Marion Island and Prince Edward Island. Seven species occur in New Zealand.

4) subg. *Lophozia* has two Austral species. *Lophozia excisa* (Dicks.) Dumort. is bipolar, in the Southern Hemisphere occurring in our area, the southernmost tip of South America, South Georgia and the Antarctic (a species from South Georgia is a synonym: *Lophozia propagulifera* (Gottsche) Steph., Sp. Hepat. 2: 139. 1901, *syn. fide* Schuster [1969c, p. 512, 521] ≡ *Jungermannia propagulifera* Gottsche in Neumayer, Deutsch. Exp. Int. Polarforsch. 2: 451. 1890). The second species is *L.* cf. *groenlandica* (Nees) Macoun (subg. *Lophozia*), and is bipolar, in the Southern Hemisphere known only from the South Orkney Islands and the western coast of the Antarctic Peninsula (Bednarek-Ochyra et al., 2000).

5) subg. *Isopaches* (Buch) R.M.Schust. has two species, both known only from our area.

6) subg. *Schistochilopsis* N.Kitag. has *L. patagonica* Herzog & Grolle from southern Chile.

7) subg. *Hypolophozia* R.M.Schust. has *L. laxifolia* (Mont.) Grolle of southern Chile and *L. argentina* (Steph.) R.M.Schust. known from Argentina (type) and South Africa (Váňa, 1982, p. 81). Only eight species occur in tropical America (Gradstein et al., 2001).

References: Schuster (1968b, 1969c, 2002a).

Key to Species

1a. Stem in cross section with medullary cells ± uniform, the ventral cells not or scarcely smaller, with or without mycorrhizae 2

2a. Underleaves consistently lacking (rarely 1–2-celled rudiments) on sterile shoots; leaves rather invariably and consistently 2-lobed; branching never consistently lateral-intercalary. Cells (except *L. pumicicola*) ± strongly, equally firm-walled, the lumina often rounded at angles; oil-bodies usually 3–4(5–15) per cell. Subg. *Isopaches* 3

3a. Plants devoid of gemmae; leaves longer than broad, ovate, the lobes often almost juxtaposed, the sinus often sharp; ♀ bracts 2(3)-lobed, the lobes sometimes with 1–2 additional teeth. Paroecious . . . . . *L. pumicicola* (p. 663)

3b. Plants copiously provided with orange-red or red-brown gemmae; leaves broader than long, suborbicular-subquadrate to suboblate, with wide, open sinuses 4

4a. Leaves consistently bilobed; leaf cells distinctly evenly thick-walled, trigones indistinct, the surface smooth or faintly papillose; stems with cortex scarcely differentiated from the medullary; gemmae polygonal to stellate. ♀ Bracts with lobes usually ± strongly toothed; paroecious or heteroecious . . . . . *L. bicrenata* (p. 665)

4b. Leaves shallowly 2–3-lobed; leaf cells in median sector of leaf thin-walled and with distinct trigones, the surface distinctly striate; stems with cortex in 2–3 rows of firm-walled, smaller cells; gemmae basically smooth, elliptic, not angular . . . . . [*Tritomaria*; p. 666]

2b. Underleaves variable in size and shape, often lanceolate, sometimes bifid, usually distinct on sterile shoots, at least at their apices; leaves bilobed, or variably 2–3(4)-lobed on one stem; branching all lateral-intercalary. Subg. *Protolophozia* 5

5a. Mature sterile (and all gynoecial) shoots with underleaves large, well developed (ca. 0.35× leaf size), subcuneate-oblong (obvious under dissecting microscope); leaves 2–3(4)-lobed to 0.4–0.75, the lobes mostly 2–3× as long as broad; cells leptodermous, lacking trigones. ?Dioecious . . . . . *L. herzogiana* (p. 648)

5b. Mature sterile shoots usually lacking underleaves or underleaves rudimentary (near apices of ♀ shoots sometimes distinct, but small) (normally appearing absent under dissecting microscope); leaves 2-lobed for 0.2–0.45 (2–3-lobed in *L. multicuspidata*); median cells usually under 38 μm broad 6

6a. Plants autoecious, paroecious or heteroecious, medium-sized, the shoots 1–1.5 mm wide × 5–30 mm long; gemmae green or vinaceous, angulate (or lacking); perianth terete below, shallowly plicate distally, mouth crenulate or denticulate with teeth 1(2) cells long 7

7a. Leaf surfaces distinctly striate-papillose; stem cortex undifferentiated; antheridial stalks uniseriate 8

8a. ♀ Bracts usually coarsely dentate; upper leaves of ♀ shoots dense, vertical; gemmae lacking; leaf lobe margins with cells 36–48 × 30–38 μm. Autoecious and frequently paroecious. Alpine, penalpine . . . . . *L. nivicola* (p. 654)

8b. ♀ Bracts with lobes edentate; upper leaves of ♀ shoots not dense, not forming a capitulum, not vertical; gemmae always present, greenish; leaf lobe margins with cells 25–35 × 21–27 μm or smaller 9

9a. Leaves ovate to suboblate, usually 1.2–1.4× as long as wide, the base weakly concave; lobes often strongly squarrose; cells with ± small trigones; oil-bodies usually 20–45 per cell. Autoecious . . . . . *L. autoica* (p. 649)

9b. Leaves oblong-falcate, narrower, often to 1.6–1.8× as long as wide, the base distinctly concave; lobes incurved but never squarrose; cells with large trigones; oil-bodies fewer, (5–8)9–15(18–24) per cell. Autoecious and heteroecious . . . . . *L. subalpina* (p. 652)

7b. Leaf surfaces smooth (or faintly striolate see *L. monoica*); stem cortex 1–2-layered; antheridial stalk 2-seriate, at least above 10

10a. Leaf lobe apices sharp, the tip cell distinctly longer than wide; stems lacking mycorrhizal hyphae; shoots medium, to 1260 μm wide. Autoecious or paroecious . . . . . *L. multicuspidata* (p. 657)

10b. Leaf lobe apices not sharp, the tip cell ± isodiametric; stems with at least some mycorrhizal hyphae; shoots small, to 840 μm wide. Autoecious or paroecious . . . . . *L. monoica* (p. 655)

6b. Plants dioecious, minute, the shoots under 0.5 mm wide × 2.5 mm long (sterile shoots only to 110 μm wide); gemmae spherical, bright red; perianth plicate/sulcate almost to base, at mouth with cilia hyaline, with a uniseriate row of to 11 cells. Epiphytic . . . *L. druceae* (p. 661)

1b. Stem in cross section with a ventral band of much smaller, mycorrhizal cells (with maturity, cells brownish, eventually disintegrating in at least part). Underleaves lacking. Cells thin-walled, with trigones minute to small; ♀ bracteole connate. Plants paroecious. Subg. *Lophozia* . . . . . *L. excisa* (p. 662)

Subg. ***Protolophozia*** R.M.Schust.

Subg. *Protolophozia* R.M.Schust., Nova Hedwigia 15: 472. 1968. Type: *Lophozia crispata* R.M.Schust.

Lophozia herzogiana E.A.Hodgs. & Grolle

Lophozia herzogiana E.A.Hodgs. & Grolle *in* Grolle, Rev. Bryol. Lichénol. 31: 152. *f. 1*. 1962. Holotype: New Zealand, North Is., N of Rotorua, near Atiamuri, 1931, *Allison* (MPN 19439 ex herb. Hodgson no. 11881); isotype: (CHR ex herb. Allison H2528!).

Plants pale green, at times red-tinged, sometimes strongly so. Stems with cortical cells poorly differentiated, feebly thick-walled, subequal to the medullary cells, a few cells with mycorrhizal hyphae; medullary cells undifferentiated, ± uniform. Rhizoids, pale, long, irregularly scattered on ventral surface of stem, with some from stem at underleaf base and ventral leaf base. Branching sparse, irregular, the branches of ventral-intercalary type. Leaves distant to contiguous, obliquely spreading, the insertion moderately to distinctly succubous, the leaves 2–3-fid to 0.5–0.75; lobes plane to a little ventrally sulcate, divergent, mostly 2–3× as long as broad, lanceolate, distinctly acute, at times somewhat apiculate, entire, terminating in a unicellular row of 2–4 cells; lamina weakly subcarinate distally, entire or sporadically with a tooth. Cells with walls thin, trigones minute or lacking, the median cells (35)40–50 μm wide; basal cells scarcely larger; surface smooth or minutely striate toward leaf base. Underleaves large, ca. 0.35× leaf size, subcuneate-oblong, bilobed to ca. 0.5, often asymmetrically so, the lobes ± acuminate, at times subapiculate, the lobe and lamina margins entire; underleaves on suboptimal shoots undivided, lanceolate and with margins entire or with a tooth. Asexual reproduction by gemmae borne on elongate, attenuated, purplish branches, with

leaves and underleaves equal in size, small and appressed, the gemmae reddish, (1)2-celled, 4–5-angled.

Dioecious? (only ♀ known). Androecia not seen. Gynoecia on leading shoots; bracts of innermost series ensheathing the perianth, free, cuneate at the base, 4-lobed to 0.35; bracteoles of innermost series bilobed, similar to bracts in size. Perianth long-exserted, cylindrical, elliptic-subfusiform, plicate in distal 0.2–0.25, contracted to the mouth, the mouth crenulate-subdentate by cells that are free only from just below the summit grading to nearly entirely free to their bases, the cells only slightly elongated, at most moderately tapering to a rounded summit; perianth bistratose in basal 0.2, the remainder unistratose.

Capsule long-exserted beyond perianth, the wall 35–45 μm thick, of (3)4 layers, the outer layer of cells with nodular thickenings; inner layer of cells with semiannular bands.

Spores brown, ca. 14 μm in diam., minutely asperulate. Elaters bispiral, ca. 7 μm wide.

Distribution and Ecology: New Zealand: South Island (620 m), North Island (300 m); Australia: New South Wales (Tinderry Mtns., 1220 m, *Curnow 4598*, CANB). Adventive in southern England (Crundwell and Smith, 1989).

Known in the North Island from an area centered on Rotorua (Whakarewarewa Hill, Atiamuri, E of Waiotapu Valley, Kaingaroa Forest); all specimens collected by K. W. Allison between 1929 and 1940 and mostly found under *Leptospermum scoparium* on rotting tussock, soil and rotting logs, but also recorded by Allison as "on vegetation in swamp" and "on dead tutu (*Coriaria*) in opening in pine forest." A specimen recorded more recently in the South Island in the Fyfe River (Marino Mtns., Western Nelson) may be this species but lacks the distinctive facies of *L. herzogiana*. It occurred on a quartzite boulder on a riverbank bordered by *Nothofagus menziesii* forest, with *Triandrophyllum subtrifidum* (*Glenny 6216*, CHR 507146).

Comments: A distinctive species in the large and conspicuous underleaves, which are ca. 0.35× leaf size. The underleaves are bilobed (at least on well-developed shoots) to ca. 0.5, often asymmetrically so. Leaves are rather deeply 2–3(4)-lobed and the cells are leptodermous. Grolle (1962b) included a useful illustration, Hodgson (1972) included an illustration (fig. 2, by T. Herzog), and Schuster (2002a, fig. 299, p. 244) provided an illustration based upon an isotype.

Lophozia autoica R.M.Schust.

[Fig. 140; Fig. 146: 3, oil-bodies, p. 672]

Lophozia autoica R.M.Schust., Nova Hedwigia 15: 479. 1968. Type: New Zealand, South Is., Otago, Morrison's Creek, Leith Valley, Dunedin, 200–300 ft., *Schuster 48593a*.

Plants loosely creeping to ascending, slender, often with an etiolated appearance, soft-textured, translucent pure green, the sterile shoots without trace of secondary pigments (♂ at times with brownish to chestnut pigments), mostly to 1.5 mm wide (slender sterile shoots often under 1 mm). Branching sparing, irregular, the branches usually lateral-intercalary from ventral half of leaf axils; *Frullania*-type branches occasional. Stems soft, slender, the cortical cells not differentiated, thin-walled, the cells similar to or (here and there) slightly larger in diameter than the medullary; medullary cells with all cells similar in diameter, without trace of dorsiventral differentiation, thin-walled, without mycorrhizal hyphae. Rhizoids frequent, long, colorless. Leaves soft-textured, translucent green, on most stems ± squarrose (with lobes

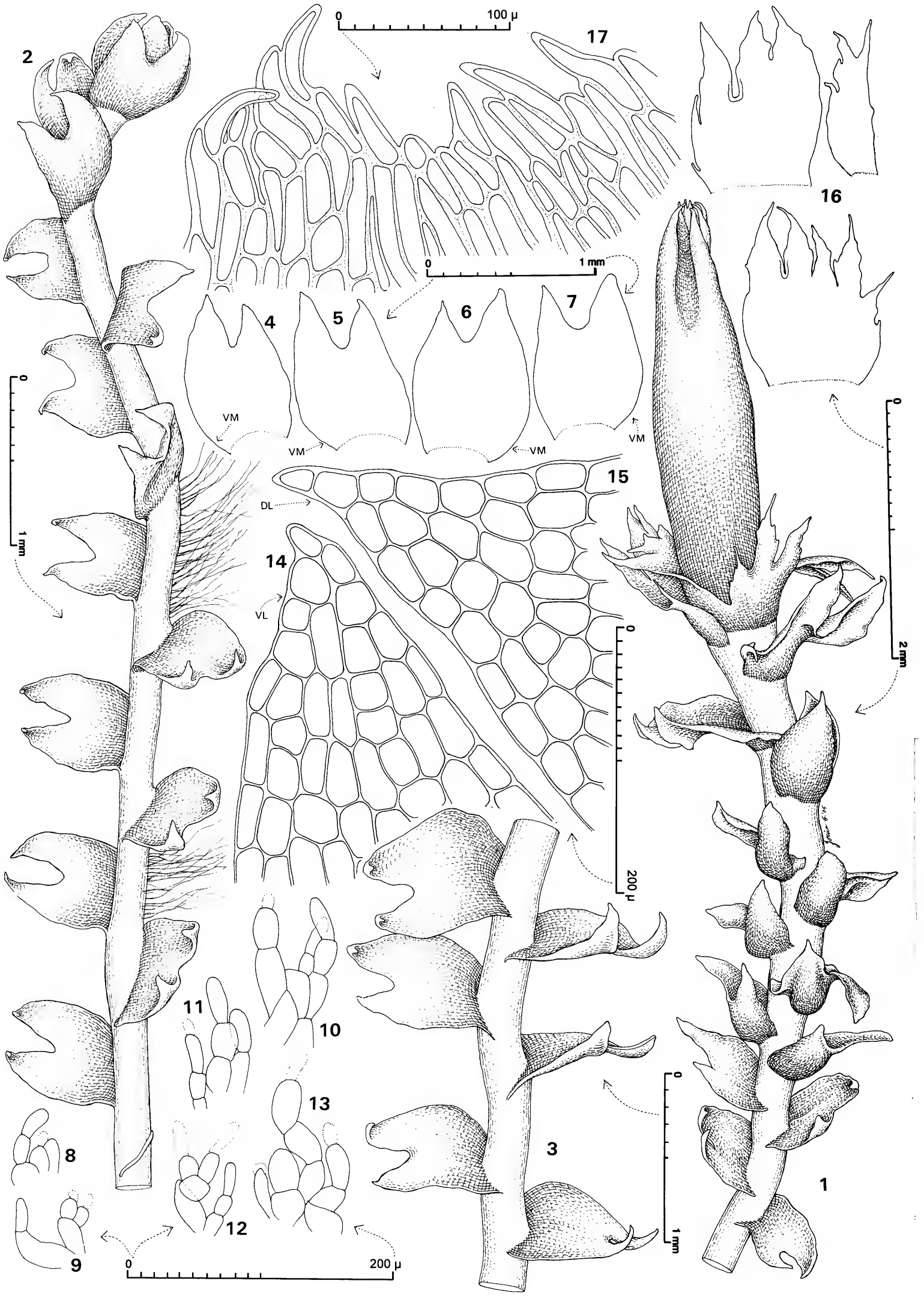

Fig. 140.
Lophozia autoica R.M.Schust. 1. Shoot showing paroecious condition, dorsal view. 2. Portion of shoot, dorsal-lateral view; note oblique leaf insertion and rhizoid distribution. 3. Portion of shoot, dorsal view. 4–7. Leaves (VM = ventral margin). 8–13. Underleaves. 14, 15. Ventral (= VL) and

often strongly squarrose, often hooked at the tip) from a spreading weakly concave base, remote (often markedly so), succubously oriented, the insertion oblique to subhorizontal; leaves asymmetrically bilobed (sporadically 3–4-lobed) to 0.35–0.4(0.45), the ventral lobe a little larger, the leaves often ovate and typically clearly longer than wide (usually 1.2–1.4× as long as wide), ca. 560–570 μm wide × 700–725 μm long, but some leaves suboblate and slightly wider than long; leaves of some axes, particularly fertile ones, atypical: then 3–4-lobed for 0.3–0.35 their length and from narrowly obtrapezoidal to oblong-obtrapezoidal, rarely one or two bisbifid for 0.4–0.55 the length, then obtrapezoidal; lobes medium to broadly acute, at times sharply so, rarely subacuminate, terminating in a single cell or a uniseriate row of 2 cells, the tip cells mostly ± isodiametric, at most slightly longer than wide, the lobe margins entire; sinuses usually crescentic to broadly V-shaped; lamina margins entire, the dorsal usually nearly straight to a little arched, the ventral moderately arched. Cells delicate, thin-walled, trigones ± small, the median cells ± oblong to hexagonal, large, 22–32(35) μm wide × 34–48 μm long; marginal cells of lobes quadrate to oblong, ca. 23–27 μm wide × 26–30(35) μm long; basal cells not or little larger, 24–28(32) μm wide × 36–50(60) μm long; surface striolate-papillose. Oil-bodies (Schuster, 1968b) small and numerous, usually 20–45 per cell, appearing almost homogeneous, but formed of minute, equal, non-protuberant, barely visible spherules, the oil-bodies mostly spherical to short-ellipsoidal, ca. 2.8–3.2 × 3.6–4 μm to 3.5–4.5 × 4–4.8 μm, a few fusiform to narrowly ellipsoidal, 3–3.5 × 6.5–8 μm, rarely to 4.5 × 9.5 μm. Oil-bodies (*Glenny 9116*) hyaline but dull, 6–10(15) per middle of lobe base, inconspicuously and indistinctly finely granular, with a cloudy appearance, the outer membrane firm, the oil-bodies globose to irregularly ovoid to elliptic. Underleaves present but reduced and very inconspicuous, consisting of a cluster of cells irregular in form, in the most reduced form comprised of 2 cells + 2 slime papillae, the underleaves occasionally present on some vigorous shoots and linear to linear-lanceolate, 1–2 cells wide and 2–5 cells long, the shoots with polymorphous, 3–4-lobed leaves sometimes with larger, lingulate underleaves. Asexual reproduction by gemmae, the gemmae greenish, subquadrate to polyhedral, with thickened, somewhat projecting angles, 1–2-celled, ca. 16–18.5 × 16–20 μm to 16–22 × 20–22 μm to 24 × 25 μm.

Uniformly autoecious. Androecia often weakly brownish to chestnut pigmented, even when remainder of plant is pure green, ± spicate, the position variable: from axils of subfloral bracts (often) or on branches arising from a leading shoot that also gives rise to gynoecial branches, or intercalary on main stems, or on subfloral innovations arising from beneath the gynoecium; bracts in 5–8 pairs, smaller than leaves, becoming remote to subcontiguous, strongly asymmetrically bilobed, with the ventral lobe spreading to squarrose, the dorsal lobe quite abbreviated, erect, the bract base ventricose; dorsal margin usually with a slender spur or cilium, often inflexed and hidden; antheridia 1 per bract, the stalk uniseriate. Gynoecia terminal on leading shoots or on elongated to somewhat abbreviated lateral-intercalary leafy branches, at times with 1–3 subfloral innovations; bracts very variable in size and form, suberect to widely spreading or even with squarrose lobes, free from each other, 3–4-lobed to ca. 0.35, subquadrate to subquadrate-obtrapezoidal, never clearly wider than long, not or weakly crispate; lobes with margins often recurved, at least toward the base, the lobes then adaxially sulcate, sharp, the apices angular to cuspidate, terminating in a single cell or a uniseriate row of 2

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dorsal (= DL) lobes of leaf (both drawn to same scale). 16. Two ♀ bracts (above and below), and to right, bracteole (abaxial aspect). 17. Portion of perianth mouth. (All from *Glenny 9116*, New Zealand, South Is., Westland EP, Mt. Brown.)

moderately elongate cells, the lobe margins usually entire, at times with 1–several accessory small teeth toward base; lamina margins occasionally with a few teeth, occasionally on each side with a lacinia; bracteoles free but very closely juxtaposed to bract on one side, variable, irregularly ovate-lanceolate and unlobed to obovate and bilobed, in either case in distal half with several cilia and laciniae, or ciliate-dentate, the lobes becoming ciliiform distally. Perianth fusiform to cylindrical-obovoid to obovoid to broadly clavate, pluriplicate in at least the distal 0.25, contracted at the mouth; mouth fringed with 2–3 tiers of strongly elongated, somewhat thick-walled cells, crenulate-dentate with projecting cells whose distal 0.3–0.5 are free, the mouth with scattered, local areas with elongated cells that are free to their base and thus locally setulose-ciliolate, the free or nearly free cells tapering, acute to acuminate, strongly elongated, mostly 60–75(80) μm long × 13–15.5 μm wide at base, some up to 85 × 16–18 μm, the apices rather thick-walled; cells below apex rapidly becoming short-oblong and more thin-walled with weak concave-sided trigones.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (930–1310 m), North Island (1230 m). Known only from Otago (Dunedin), Canterbury (Arthur's Pass), Westland (Mt. Brown, Otira River) and Volcanic Plateau (Mt. Ruapehu) EPs.

The species was found in a protected niche over humus on a bank along a small stream in a forest dominated by *Nothofagus solandri* var. *cliffortioides* at ca. 1230 m along the Blyth Track (Tongariro Natl. Park, Wellington). While Schuster (2002a, p. 258) keys this species as one of the "Forest zone," we have discovered that the plant has a broader ecological range. For example, it occurs in penalpine scrub on a steep-sided slope of the Upper Twin Creek Valley (Arthur's Pass, 930 m). Also over soil at the side of a rill at 1210–1310 m in a mosaic of alpine tussock grass, rills and small rocky outcrops (Otira Valley Track, Arthur's Pass), and on Mt. Brown (central Westland, 1080 m) in a south-facing ditch under shrubland of *Hebe subalpina*, *Dracophyllum longifolium*, *D. rosmarinifolium*, *Chionochloa rubra* and *Celmisia armstrongii*, with *Bazzania involuta*, *Breutelia elongata*, *Clasmatocolea* sp., *Plagiochila retrospectans*, *Ptychomnion aciculare* and *Riccardia pennata*. The type occurred admixed with *Trichocolea mollissima*, *Balantiopsis* sp., *Haplomitrium gibbsiae* and *Heteroscyphus fissistipulus* (Schuster, 1968b).

Comments: The species is often fertile, and in our experience mostly paroecious (Fig. 140: 1), although not exclusively so. The leaves are frequently distant, lending a rather "etiolated" appearance to the plants (Fig. 140: 2). Leaves are concave, with incurved to "claw-like" lobe tips, and the tip cells of the lobes are never elongated (Fig. 140: 3). The species superficially appears similar to *Lophozia multicuspidata* in the general leaf form and shape, including lobes that terminate in a single cell or a uniseriate row of 2 cells. *Lophozia autoica* differs from that species in the striate-papillose leaf surface, the isodiametric tip cell of the lobe (or at most slightly longer than wide), the frequent presence of gemmae and the uniseriate antheridial stalks vs. the smooth surface, the sharp lobe apices with the tip cell distinctly longer than wide (to 3:1), the lack of gemmae and the biseriate antheridial stalks, at least above.

Lophozia subalpina (R.M.Schust.) R.M.Schust.

Lophozia autoica var. *subalpina* R.M.Schust., Nova Hedwigia 15: 482. 1968. *Lophozia subalpina* (R.M.Schust.) R.M.Schust., Beih. Nova Hedwigia 119: 263. 2002. Type: New Zealand, South

Is., Fiordland, Humboldt Mtns., track from Lake MacKenzie to Harris Saddle, ca. 3800 ft., *Schuster 67-3888a.*

Plants light green, distal parts of leaves and bracts often ± brownish to purplish brown. Branching sparse, the branches ventral- and lateral-intercalary. Leaves subvertical, rather widely spreading, concave, with incurved (but never squarrose) lobes, usually all 2-lobed to 0.3–0.35, rarely 3-lobed, oblong-falcate, often to 1.6–1.8× as long as wide, ca. (390)400–425(450) μm wide × 635–735(775) μm long; lobes sharply acute (at times long-acute), terminating in a single or (sporadically) a uniseriate row of 2 cells, the tip cell of the lobes ± isodiametric or at most a little elongated, the lobes rather frequently terminating in 2 laterally juxtaposed cells; lamina with dorsal margin straight to weakly incurved, the ventral evenly, moderately arched, the margins ± parallel. Cells in median sector of leaf with well-developed but usually not perceptibly bulging trigones, the cells in lobe apices strongly collenchymatous with bulging, usually confluent trigones, the median cells 16–24 μm wide × 24–36 μm long to 22–30 μm wide × 26–43 μm long, usually conspicuously oblong and with the lumina rounded; surface distinctly striate-papillose. Oil-bodies colorless (Schuster, 1968b), (5)9–15(24) per cell, faintly granular-botryoidal, spherical and 3–4.5 μm in diam. or ellipsoidal and 5 × 7(11) μm. Underleaves reduced and inconspicuous, polymorphous, often of only a few cells, at times consisting of a base of 2 cells wide + 2 lobes each of a uniseriate row of 2 cells capped by a slime papilla. Asexual reproduction by gemmae, the gemmae sporadic, pale green, rarely faintly reddish, stellate to quadrate, 17 × 17 μm in diam. to 20–22 × 21–24 μm, 1–2 celled.

Paroecious and autoecious. Androecia intercalary, bracts in 3–5 pairs, laxly imbricate, leaf-like except moderately ventricose at base, with a strong tooth at the dorsal base; antheridia 1 per bract, the stalk uniseriate. Gynoecial bracts erect and sheathing the perianth, those of innermost series often dimorphic: one bilobed to 0.35–0.4, the other 3–4-lobed to 0.25–0.4, the lobes acuminate to ± cuspidate, terminating in a single cell or a uniseriate row of 2 cells, the tip cell ca. 2:1, sharp at the summit, the lobe margins entire, rarely with a tooth; lamina margins repand, entire or with a large tooth on the dorsal margin; bracteole free, 3-lobed to ca. 0.24, the lobes narrowly acuminate, terminating in a uniseriate row of 2–3 cells, the tip cell ca. 3:1, sharp at the summit. Perianth cylindrical, contracted toward the plicate mouth, the mouth shallowly lobulate, the lobules distally with elongated cells, ca. 14–16 × 40–50 μm isolated cells to 15 × 82 μm, projecting to form crenulations, locally the terminal cells free and thus locally setulose-ciliolate.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1160–1435 m).

Known from only a few collections. Occurring in a mosaic of scrub and grassy areas near Temple Basin Skifield (Arthur's Pass). Also over soil in the alpine zone at 1280–1330 m along Stocking Stream (Mt. Cook Natl. Park). The type occurred over peaty soil, on boggy ground in the penalpine zone among *Chionochloa.*

Comments: This species differs from the related *Lophozia autoica* by the larger, more conspicuous trigones, the narrower leaves that are oblong and often 1.6–1.8× as long as wide, the less strongly incurved leaf lobes, and the fewer oil-body number per cell (5–8)9–15(18–24) vs. the ± small leaf cell trigones, the broader leaves that are ovate to suboblate and usually 1.2–1.4× as long as wide, the often strongly squarrose lobes, and the larger oil-body number per cell (20–45) in *L. autoica*. *Engel 6458A* from Temple Basin has both paroecious and autoecious plants.

Schuster (2002a, fig. 309, p. 267) illustrated plants based on *Schuster 67-455*; that collection was cited in Schuster (1968b) as a paratype (Mt. Brewster, Westland, 1435 m). Several characters deviate from the concept of the species *sensu* the protologue, e.g., leaf shape, bract lobe number. Also, Schuster (1968b, p. 483) was unable to establish the sexuality of the type of *Lophozia autoica* var. *subalpina*, but stated that *Schuster 67-455* contained both autoecious and heteroecious plants. We have not included characters derived from the paratype in the species description here, especially since Schuster (2002a, p. 266) remarked "it is possible that RMS 67-455 represents an extreme of *L. nivicola*."

Lophozia nivicola R.M.Schust.

Lophozia nivicola R.M.Schust., Nova Hedwigia 15: 477. 1968. Type: New Zealand, South Is., Mt. Brewster, NE of Haast River, 4700 ft., *Schuster 67-455c*.

Plants green, becoming whitish with age, the ♂ bracts tinged with reddish brown, shoots small, to 1.5 mm wide, 12 mm long. Branching sporadic, the branches exclusively lateral-intercalary; stolons lacking. Stems with cortex undifferentiated; medullary cells undifferentiated, ± uniform and lacking mycorrhizal hyphae. Leaves subvertical to subhorizontal, remote below, on fertile shoots usually dense and crowded distally, subvertical to vertical, erect-spreading and lobes ± spreading; leaves ovate to ovate-oblong, slightly asymmetric, bilobed to 0.35–0.4 (often a few trilobed on fertile shoots), 720–880 μm wide × 1075–1225 μm long; lobes cuspidate, always very sharp, terminating in 1–2 elongated cells, the lobe margins entire; sinus V-shaped and usually with a rounded base, not gibbose; lamina margins arched, the ventral usually more strongly so, typically entire but sporadically with a tooth. Cells with walls thin, with trigones distinct, mostly concave-sided, the median cells (26)28–38(42) μm wide × 35–48(52) μm long; apical cells large, 36–48 × 30–38(42) μm; surface faintly papillose. Oil-bodies (Schuster, 1968b) colorless, usually 16–25 per cell, finely granular, ellipsoidal to fusiform, 4–5 × 6 to 5–5.5 × 7–10 μm, a few to 6 × 7–8 μm. Underleaves lacking on sterile shoots. Asexual reproduction by gemmae, the gemmae at least sporadically present, greenish, 1-celled, polygonal.

Heteroecious: autoecious and (frequently) paroecious. Androecia with bracts often ± brownish red, in (1)2–3 pairs, ventricose at dorsal base; antheridia 1 per bract, the stalk uniseriate. Gynoecia with bracts variable, always strongly spinose-dentate (the teeth distinct even on 2–3 pairs of subfloral leaves); bracts of innermost series mostly subquadrate, 3–4(5)-lobed to 0.35–0.45, the lobe apices sharply cuspidate, the tip cell 30–32 × 110–125 μm, the margins conspicuously spinose-dentate; lamina margins spinose-dentate; bracteole free or essentially so, oblong to obcuneate, usually bifid to 0.3–0.45, dentate-like bracts. Perianth cylindrical, rather shallowly plicate distally, moderately contracted toward the mouth, the mouth lobulate, the lobules crenulate-denticulate with elongate sharp cells that are thick-walled and free at their tips or free for their entire length, the longer cells 24–25 × 80–108 μm; perianth surface below mouth occasionally subhispid or tuberculate with isolated protruding cell tips.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (1435 m), known only from the type. The type is from the penalpine tussock zone mixed with *Austrolophozia paradoxa*, "*Riccardia mammillosa*," *Pachyschistochila altissima*, *Haplomitrium gibbsiae*, *Lophozia autoica* and *Metzgeria atrichoneura* (Schuster, 1968b). The type is the only collection cited in the literature (see Schuster, 2002a, p. 263).

Comments: Schuster (2002a, p. 266) remarked *Lophozia nivicola*, *L. autoica*, *L. subalpina* and *L. androgyna* of Tasmania formed a "difficult complex" and "of these taxa, *L. nivicola* and *L. subalpina* appear to stand apart because leaf lobes tend to be clearly cuspidate…with lobe tips formed by elongated, sharp cells." See Schuster (2002a, figs. 307, 308) for illustrations.

Lophozia monoica (E.A.Hodgs.) J.J.Engel

[Fig. 141; Fig. 146: 4]

Metahygrobiella monoica E.A.Hodgs. of New Zealand, Trans. Roy. Soc. New Zealand, Bot. 3: 76. 1965. *Lophozia monoica* (E.A.Hodgs.) J.J.Engel, Novon 17: 311. 2007. Holotype: New Zealand, South Is., Fiordland, mountains above Nancy Sound, 3600 ft., Jan. 1963, *Burrows s.n.* (MPN, herb. Hodgson no. 12548!); isotype: (CHR – *absens*).

Plants golden brown, the leaf lobes and ♂ bracts at times tinted with rose, rather flaccid, shoots small, to 840 μm wide. Stems with cortical cells numerous, in 1(2) layers of firm-walled cells, the cells similar to the medullary in size or a little smaller, the ventral cortical cells not smaller, with mycorrhizal hyphae in some cells, a hyaloderm completely absent; medullary cells numerous, thin-walled. Branches (vegetative) not seen. Leaves suberect to obliquely spreading, feebly dorsally assurgent, contiguous, succubously oriented and inserted, ovate to short-subrectangular, mostly 2-, sporadically 3-lobed to 0.3–0.35, the lobes medium to broadly acute, tapering to the tip but the summit not sharp, the lobes terminating in a single subisodiametric cell that is rounded at the summit. Cells of leaf with trigones present, distinct, small and concave-sided to medium and straight-sided, the cells at lobe base 24–30 μm wide × 23–36 μm long, the median cells 22–29 μm wide × 30–40 μm long; surface faintly striolate. Underleaves (vegetative shoots) present, reduced and inconspicuous, free but closely juxtaposed to leaf base, few- to several-celled, at times feebly lamella-like and consisting of several tiers of cells, often with a uniseriate row of 2–3 cells. Asexual reproduction ?absent.

Plants paroecious or autoecious (with ♂ on a subfloral innovation), ♂ bracts below perianth with the inflexed, lobule-forming margin with a tooth distally; bracts on androecial branch contiguous, bilobed, the lobes broadly acute, the entire bract strongly ventricose-cucullate, the basal portion notably inflated and crenate in profile by distinctly bulging cells; antheridia 1–2 per bract, the stalk 2–3-seriate. Gynoecial bracts not crowded, 3–4-lobed, the lobes medium acute, subequal or the ventral a little smaller, the lobes with entire margins; bracteole present, narrow, ca. 0.3–0.5 the perianth width, connate to 0.6 with bract on 1 side, bifid to ca. 0.45 by sharply acute lobes. Perianth elongate fusiform-cylindrical, narrowing rather abruptly toward the contracted mouth, plicate only in sector just below the mouth, the mouth denticulate to spinose-dentate by cells that are free only from just below the summit grading to nearly entirely free to their bases, the cells somewhat elongated, 60 × 12 μm ranging to 96 × 19 μm (4.5–6.1:1), notably thick-walled, rather sharply angled to the summit or the summit narrowly rounded.

Seta seen only in collapsed state. Capsule not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1100 m). Known from Fiordland EP.

Known only from the type; plants occurred admixed with *Riccardia* sp.

Comments: The species has been mentioned in the literature only a few times since described

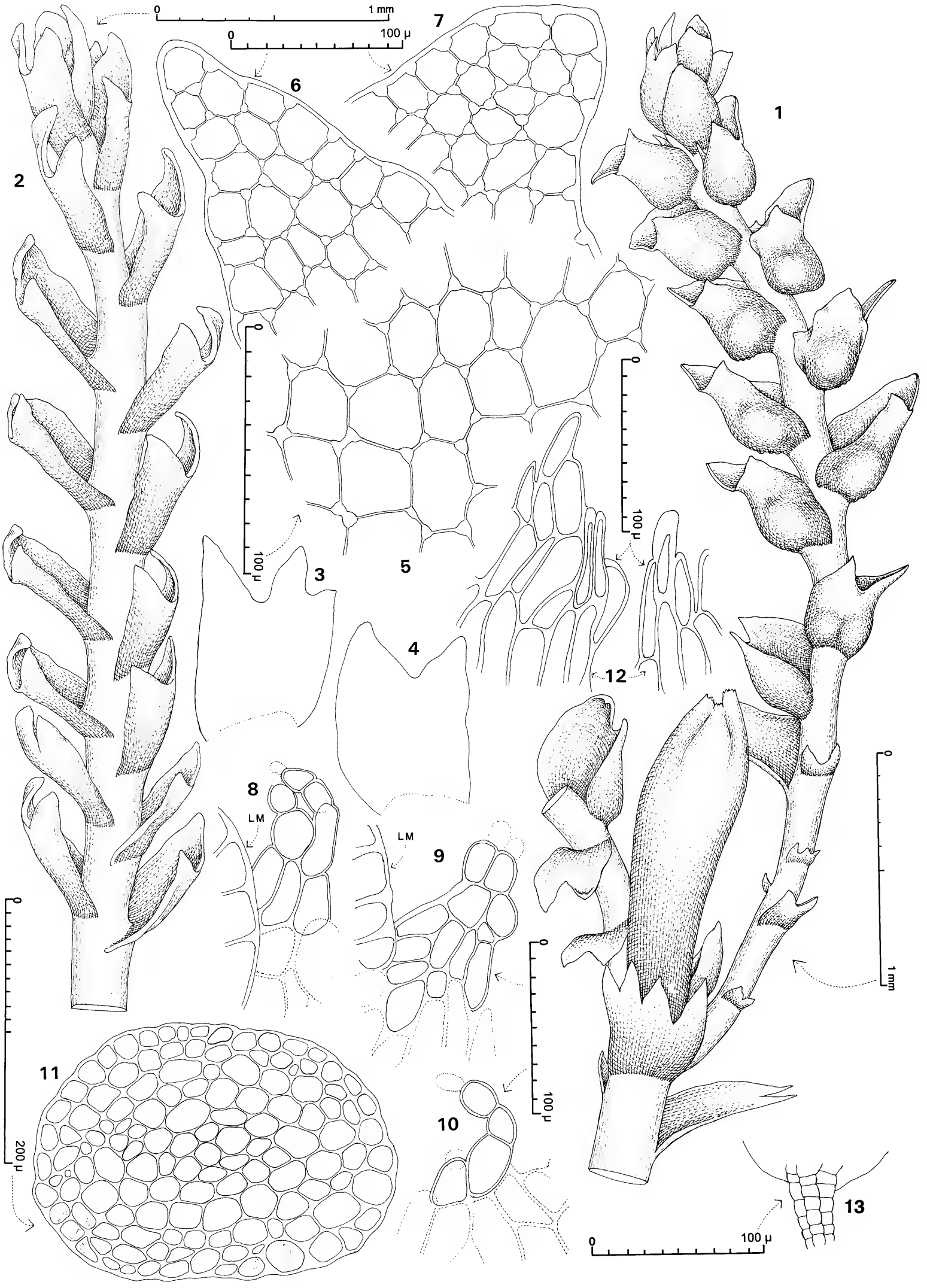

Fig. 141.
Lophozia monoica (E.A.Hodgs.) J.J.Engel. 1. Portion of shoot showing paroecious condition, the 2 androecial branches arise as subfloral innovations (note the dorsal appendage on 2 distal androecial bracts). 2. Portion of shoot, dorsal view. 3, 4. Leaf outlines (drawn at same scale as figs.

by Hodgson, and comments were solely those expressing uncertainty of taxonomic position. Schuster (1969c, p. 88; 2002a, footnote p. 13) mentioned that the species was not a *Metahygrobiella*, but did not indicate its disposition.

Lophozia monoica is tentatively placed in subg. *Protolophozia*; a more definitive placement should await the discovery of vegetative branches. These were not observed in type material. The species is similar to *L. multicuspidata* in the smooth leaf surface, the 1–2-layered stem cortex (Fig. 141: 11), the biseriate antheridial stalks (Fig. 141: 13) and the autoecious or paroecious condition (Fig. 141: 1). It differs from that species in the ± isodiametric tip cell of the leaf lobes (Fig. 141: 6, 7), which is less sharp than in *L. multicuspidata*, the presence of at least some mycorrhizal hyphae in stem cells (Fig. 141: 11) and the smaller shoot size (to 840 μm wide). *Lophozia multicuspidata*, on the other hand, has apices of leaf lobes sharp, with the tip cell distinctly longer than wide (Fig. 142: 7, 8), stem cells without mycorrhizal hyphae (Fig. 142: 14) and a larger shoot size (to 1260 μm wide).

The description of this species is based solely on the type. However, we tentatively refer two collections to this species and briefly discuss them here. The first is from Mt. Brown (Westland EP, 1080 m, *Glenny 9110*, CHR 571758), which has only intercalary branching, mostly lateral and only a single ventral. Oil-bodies were illustrated from this plant (Fig. 146: 4); the data follows. Oil-bodies occupying a large portion of cell volume, opaque, light smokey grey, 9–17 per median cell of lamina, finely papillose, the spherules slightly protruding beyond membrane, the oil-bodies notably irregular in shape, globose to elliptic to fusiform to paramecioid and with one or both ends sharp-pointed to potato-shaped, some triangular in profile. At the Mt. Brown site plants occurred in a ditch on a south-facing slope on the surface of a bolster of *Sphagnum cristatum*, with *Clasmatocolea humilis*, *Lepidozia obtusiloba* and *Riccardia lobulata* under shrubs of *Hebe subalpina*, *Dracophyllum longifolium*, *D. rosmarinifolium*, with *Chionochloa rubra* and *Celmisia armstrongii*.

The second (Great Moss Swamp, Otago EP, 900 m, *leg. G. A. M. Scott*, CHR 422491) has only lateral-intercalary branches. The plants were found on the edge of a flush through tussock grassland, with *Chiloscyphus bispinosus*, *Marchantia foliacea*, *Polytrichum commune* and *Riccardia aequicellularis*.

Lophozia multicuspidata (Hook.f. & Taylor) Grolle

[Fig. 142]

Jungermannia multicuspidata Hook.f. & Taylor, London J. Bot. 3: 375. 1844. *Cephalozia multicuspidata* (Hook.f. & Taylor) Steph., Sp. Hepat. 3: 316. 1908. *Triandrophyllum multicuspidatum* (Hook.f. & Taylor) E.A.Hodgs., Rec. Domin. Mus. 4: 103. 1962. *Lophozia multicuspidata* (Hook.f. & Taylor) Grolle, Rev. Bryol. Lichénol. 31: 155. 1962. Type: Campbell Is., *Hooker*.

Plants procumbent, whitish pale green, rusty red in sun forms, medium, to 1260 μm wide. Branching infrequent, the branches lateral-intercalary, from near ventral sector of leaf axils, the branches often stoloniform. Stems soft-textured, the cortex hardly defined, in 1–2 layers, the cells somewhat smaller than the medullary cells; medulla with cells undifferentiated,

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1, 2). 5. Median leaf cells. 6, 7. Leaf lobes. 8–10. Underleaves (stippled cells = stem cells; LM = leaf margin); all drawn to same scale. 11. Stem, cross section (note mycorrhizal hyphae in a few cells in ventral sector). 12. Portions of perianth mouth. 13. Antheridial stalk. (All from type.)

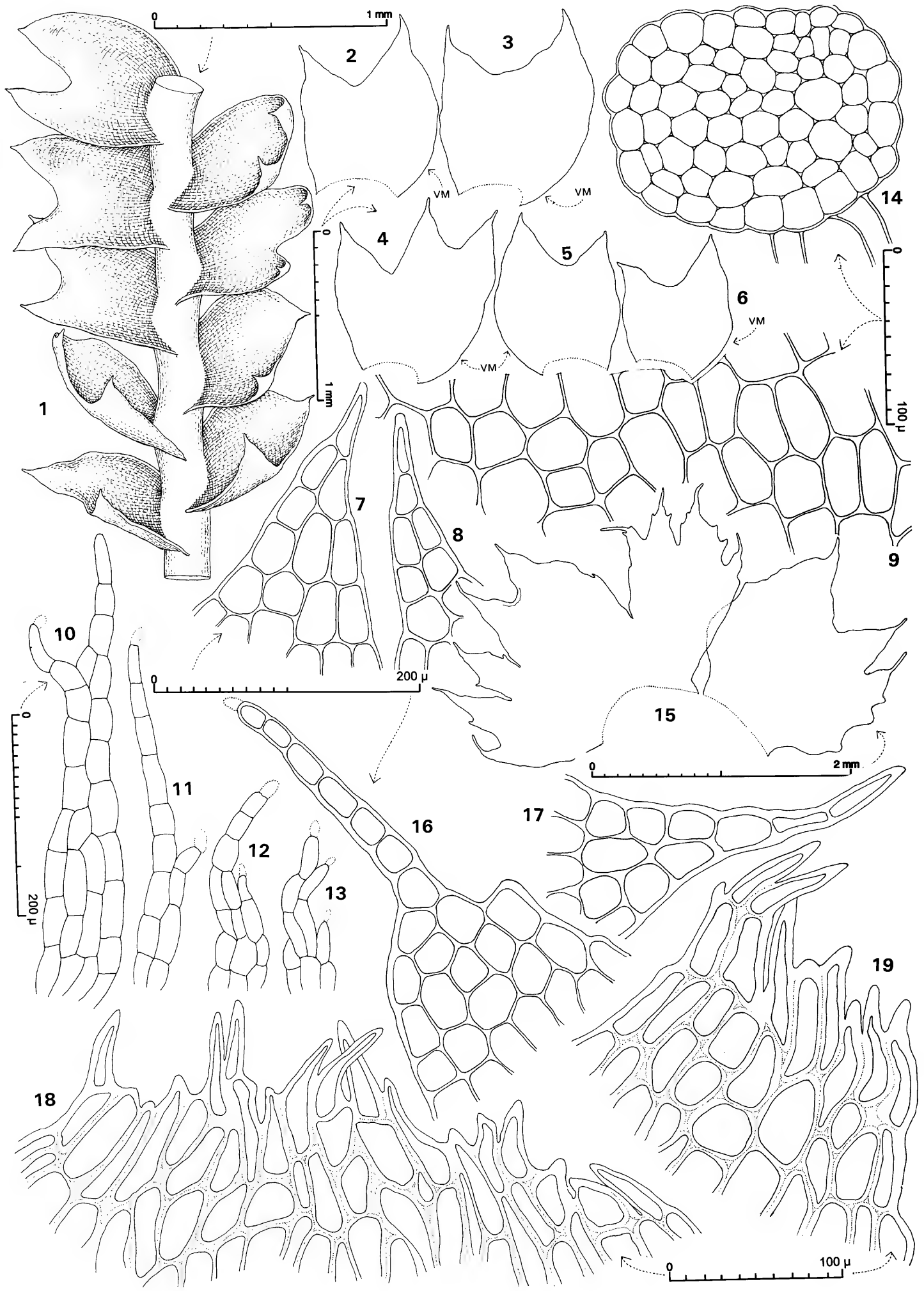

Fig. 142.
Lophozia multicuspidata (Hook.f. & Taylor) Grolle. 1. Sector of sterile shoot, dorsal view. 2–6. Leaves (VM = ventral); all drawn to same scale. 7, 8. Distal sectors of leaf lobes. 9. Median leaf cells. 10–13. Underleaves. 14. Stem, cross section. 15. ♀ Bracts and, in middle, bracteole. 16, 17. Portions of lobes of 2 ♀ bracts. 18, 19. Portions of perianth mouth; note thick-walled cells. (All from *Engel 21430*, New Zealand, Marlborough near boundary with Nelson Prov., Mt. Richmond Forest Park, Red Hills, track to Maitland Hut.)

homogeneous, lacking mycorrhizae. Rhizoids many, scattered on ventral face of stem. Leaves somewhat dorsally assurgent, widely spreading, distant to contiguous, the insertion strongly succubous, the leaves at times narrow, ovate to short-elliptic to oblong to oblong-obcuneate, the ventral margin more strongly arched than the dorsal, the leaves 2–3(4)-lobed to 0.4, the lobe number polymorphous; lobes subdivergent, acuminate, sharp, terminating in a single cell or a uniseriate row of 2 cells, the tip cell distinctly longer than wide (to 3:1); sinuses sharply V-shaped, occasionally broadly rounded. Cells thin- to firm-walled, with trigones conspicuous or small and concave-sided, the median cells large, 24–36 μm wide × 34–45(48) μm long; surface smooth. Underleaves present, very inconspicuous, ca. 0.3× stem width, short and lamella-like or more often long-lanceolate, (2)4–5 cells wide at base and tapering to a single elongated cell or more often a uniseriate row of to 6 typically elongated cells, the margins entire or with a tooth near the summit. Asexual reproduction absent.

Autoecious or paroecious, the androecia on leading shoots and with ♀ on rather short branches or the androecia on branches originating below gynoecia. Androecia at times purplish, terminal but becoming intercalary, the bracts strongly asymmetrically bilobed, the ventral lobe acute, often apiculate, tapering to a sharp tip, the dorsal lobe inflated-ventricose toward the base and with the margin incurved to form a pouch, the lobe acute distally and tapering to a sharp tip, the saccate portion crenulate in profile by way of inflated cells; antheridia 1 per bract, the stalk 2-seriate above, uniseriate below; paraphyses lacking. Gynoecial bracts 3–4-lobed, concave toward the base, but the lobes often recurved distally, the lobes acuminate to cuspidate, with margins often recurved (the lobes then adaxially sulcate), entire or with 2 small, opposing teeth, the lobes terminating in a single rather elongated cell or uniseriate row of to 4(7) elongated cells, the tip cell rather sharp; bracteole large and conspicuous but smaller than bracts, free or connate on one side, 2-lobed, or if 4-lobed then the median pair much larger, the lobes as for bracts. Perianth fusiform-ellipsoidal, plicate distally, gradually contracted in distal 0.5–0.25, the mouth crenulate-dentate by thick-walled cells that are free for varying distances, a few nearly entirely free to their bases, the cells rather elongated, tapering to a rather sharp, thick-walled summit; perianth 3–4-stratose toward base, unistratose distally; cells below the perianth mouth thin- to somewhat firm-walled and with distinct trigones with their sides straight to slightly bulging.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: Campbell Island, South Island (700–920 m).

A collection from Red Hills (Mt. Richmond Forest Park, Marlborough, ca. 700–920 m, *Engel 21430*) occurred on the floor of a bryophyte-covered slope.

Comments: This species may be recognized by the combination of several characters: the sharp leaf lobe apices, with the tip cell distinctly longer than wide (to 3:1) and tapering to a sharp summit; the large leaf cells, with median cells 24–36 μm wide × 34–45(48) μm long; the smooth leaf surface; the strictly lateral-intercalary branches from the ventral extreme of the leaf axil; the soft-textured stem, with an ill-defined stem cortex; and the autoecious inflorescences, with androecial branches originating below the gynoecia.

Underleaves are noted as absent by Hooker and Taylor (1844a), Grolle (1962b) and Schuster (1968b). However, the Red Hills specimen (*Engel 21430*) has distinct underleaves, but they are very inconspicuous, buried among the rhizoids, and may be easily overlooked. The underleaves are mostly long-lanceolate, (2)4–5 cells wide at base and taper to the summit a single cell or, more often, a uniseriate row of to 6 typically elongated cells (Fig. 142: 10–13).

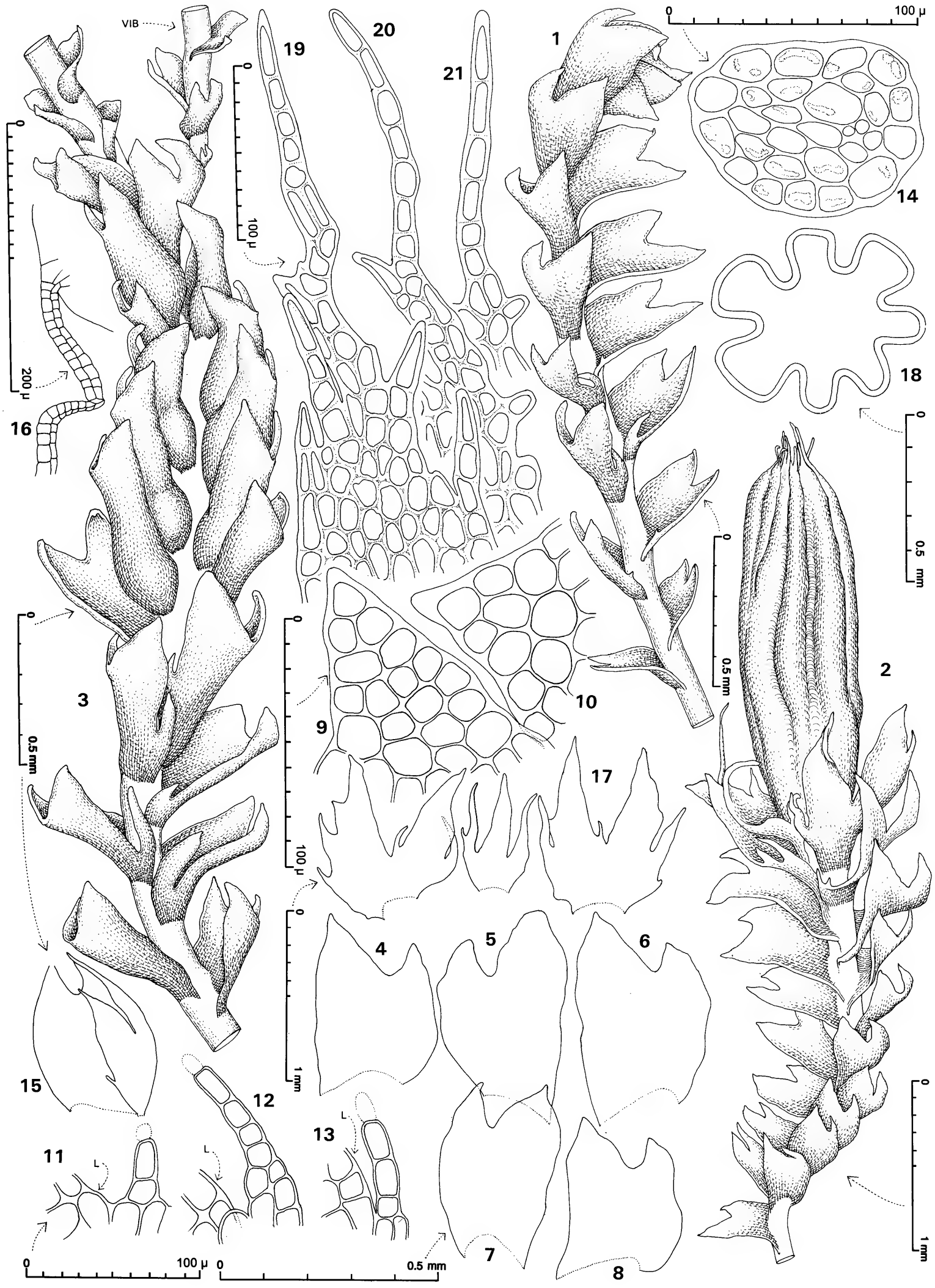

Fig. 143.
Lophozia druceae Grolle & E.A.Hodgs. 1. Sector of shoot, dorsal-lateral view; note that some leaves (incipient ♂ bracts) have a dorsal tooth but are without suggestion of becoming saccate at the base. 2. Shoot with perianth, dorsal view. 3. Portion of leading shoot with an intercalary androecium, dorsal view; note 2 ventral-intercalary branches (= VIB) near distal end of androecium;

This population has small trigones similar to those illustrated by Schuster (2002a, fig. 303: 12, p. 254).

Lophozia druceae Grolle & E.A.Hodgs.

[Fig. 143]

Lophozia druceae Grolle & E.A.Hodgs. *in* E.A.Hodgs., J. Roy. Soc. New Zealand 2: 112. *f. 1*. 1972. Holotype: New Zealand, North Is., Mt. Pukeamaru, E. Cape, Sept. 1959, *Alison C. Druce* (MPN 19436 ex herb. Hodgson herb. no. 11442!).

Plants procumbent to suberect, pale yellow-brown, especially the shoots that are not exposed, but with exposure the plants often reddish tinged; sterile plants rare, the shoots typically ♂, sporadically ♀, the sterile shoots smaller than the fertile ones, the sterile ones minute to small, 85–110 μm wide, to 2.5 mm long. Branching very sparing, often in vicinity of androecia, mostly ventral-intercalary, less often lateral-intercalary. Stems 5–6 cells high, the cortex in a single layer of thick-walled cells, the exposed wall especially so; medullary cells undifferentiated, ± uniform, of firm-walled cells; cortex and medulla with most cells infected by mycorrhizae. Rhizoids scattered, not dense, present even toward shoot apices. Leaves distant to loosely imbricate, obliquely to widely spreading, dorsally assurgent, subsuccubously oriented, the insertion succubous, bilobed to 0.2–0.35, often asymmetrically so (the dorsal lobe somewhat larger); lobes ± parallel and not divergent, medium acute, usually tapering to 1 or more biseriate tiers and then a single, subisodiametric cell that tapers to the summit, the lobe apex exceptionally narrowly rounded. Cells with walls thin, with trigones present, small to medium and straight-sided, the median cells subisodiametric, 16–23 μm wide and long; surface distinctly striate-papillose. Underleaves present, reduced and inconspicuous, free but closely juxtaposed to leaf base or connate, few- to several-celled, consisting of a tier of 2–3 cells wide and a uniseriate row of 2–4(6) isodiametric to somewhat elongate cells, at times ± ciliiform. Asexual reproduction rare, by spherical, bright red gemmae.

Dioecious. Androecia frequently produced, terminal but becoming intercalary on leading shoots (often repeatedly so), only slightly narrower than sterile sectors of shoot; bracts deeply concave, especially below, the apex shallowly bilobed; dorsal margin somewhat dilated, inflexed, with a distinct, tapering accessory lobule that tapers to the summit; antheridia 1 per bract, the stalk to ca. 24 cells long, biseriate. Gynoecia with innermost series of bracts much larger than leaves, bilobed to ca. 0.7–0.8, the lobes subsymmetric or the dorsal a little larger, the lobes narrowly attenuate to subacuminate, the margins entire or with a few teeth or laciniae, the lamina margins each with 1 lacinia or lobule and, at times, also with a small tooth toward the base; bracteole free from and smaller than bracts, unlobed and with a laciniiform-lobuliform process on each side or similar in shape and form to bracts. Perianth large for plant size, reddish, subfusiform, plicate nearly to base, markedly and sharply contracted at the

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note also that most non-ventricose leaves have a prominent tooth or lacinia near dorsal base (note that figure is drawn at same scale as fig. 1, a sterile shoot). 4–8. Leaves. 9, 10. Distal sector of dorsal leaf lobes (drawn to same scale). 11–13. Underleaves (L = leaf). 14. Stem, cross section of sterile shoot; note mycorrhizal infection of both cortical and medullary cells. 15. ♂ Bract. 16. Antheridial stalk. 17. ♀ Bracts and, in middle, bracteole. 18. Cross section through median sector of perianth. 19–21. Distal sector of lobes of perianth mouth (drawn to same scale). (All from type.)

mouth, the mouth lobulate, the lobules with hyaline, often contorted cilia, the cilia terminating in a uniseriate row of to 11, firm-walled cells, the tip cell rather elongate and tapering to the summit, the cilia with a few sharp teeth below the uniseriate sector.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: North Island. Known only from the type, which was corticolous and associated with *Chandonanthus squarrosus*, *Drepanolejeunea aucklandica*, *Plagiochila circinalis* and *Frullania* sp.

Comments: This is our only confirmed dioecious species. (*Lophozia herzogiana* may also be dioecious, but only gynoecia are known for that species.) Also, this is not only our only epiphytic species, but it is among the smallest, the shoots are minute, with sterile shoots to only 110 μm wide. Perianths are distinctive, with plicae extending from the perianth summit nearly to the base (Fig. 143: 2), and the mouth is fringed with hyaline cilia that terminate in a uniseriate row of up to 11 cells (Fig. 143: 19–21).

Subg. ***Lophozia***

Lophozia excisa (Dicks.) Dumort.

Jungermannia excisa Dicks., Fasc. Sec. Pl. Crypt. 11. 1793. *Lophozia excisa* (Dicks.) Dumort., Recueil Observ. Jungerm. 17. 1835. Type: England, Holt and Edgefield heaths, *Dickson*.
Jungermannia propagulifera Gottsche *in* Neumayer, Deutsch. Exp. Int. Polarforsch. 2: 451. 1890, *syn. fide* Schuster (1969c, p. 512, 521). *Lophozia propagulifera* (Gottsche) Steph., Exped. Antarct. Belge. Bot. 3, 4. 1901 (Sept.); Sp. Hepat. 2: 139. 1901 (Oct.). Lectotype (*fide* Grolle, 1972d): South Georgia, Bachground overhalb der Pinguinbay, *Will*.

Plants variable in size and appearance, fleshy, soft-textured or flaccid, prostrate to suberect, pale to dark green or yellow-green, or tinged, especially above, with bright red, vinaceous-red, purplish red, purple, reddish brown or brown. Stems fleshy, the cortex weakly differentiated, the cells thin-walled, slightly smaller than or subequal to the dorsal medullary cells; medulla differentiated, the cells in dorsal portion larger, leptodermous, colorless, those in ventral portion smaller, with age strongly mycorrhizal and brownish. Rhizoids hyaline, numerous, scattered on ventral surface to shoot apex, long. Branching sparing, the branches of lateral-intercalary type. Leaves soft-textured and rather delicate, often somewhat undulate, spreading, distant to contiguous, succubously oriented, the insertion distinctly succubous, somewhat asymmetrically ovate to broadly ovate-quadrate, when well developed slightly wider than long, typically weakly asymmetrically bilobed to 0.2–0.25 (the dorsal usually slightly smaller), at times divided to 0.35; lobes broadly acute, obtusely apiculate to rather sharply angular, entire; sinus shallow and crescentic; dorsal and ventral margins arched, the ventral margin somewhat more strongly so, particularly above the somewhat dilated ventral base, the margins entire (except near ♂ bracts, then often with a dorsal tooth). Cells thin-walled and with trigones minute to small, median cells 25–30 μm wide × 30–35(40) μm long, the cells of lobe margins 23–28 μm in diam.; surface smooth. Oil-bodies (*fide* Schuster, 2002a) (10)12–22(24) per cell, granular-botryoidal, spherical to ovoid. Underleaves lacking. Asexual reproduction via gemmae, the gemmae (in ours) typically present, bright red, 1–2-celled, polygonal, thin-walled but often with 1–2 angles acutely drawn out into thick-walled tips; gemmae producing shoots and leaves hardly modified, the leaf margins not becoming erose-lacerate. Fungal partner a basidiomycete.

Paroecious. Androecia with bracts in 2–4(5) pairs, similar to leaves but somewhat larger and more erect, only slightly saccate, with a tooth somewhat above dorsal base; antheridia 1–2(3) per bract, the stalk uniseriate. Gynoecia usually with 1–several subfloral innovations; bracts larger than leaves, somewhat sheathing perianth at base, the margins crispate, slightly to much broader than long, irregularly 3–5-lobed, the lobe margins entire or sporadically with a few small teeth; bracteole much smaller than bracts, often connate on one or both sides for up to 0.5, oblong to lanceolate. Perianth ca. 0.5–0.75 emergent, cylindrical-clavate, strongly plicate in distal 0.3–0.5, contracted to mouth; mouth shallowly lobed, the lobes with marginal cells notably weakly differentiated, crenulate by firm-walled cells that are free only at distal ends + a few cells projecting as blunt, short teeth rounded at the summit.

Capsule ovoid, the wall 3–4-stratose; outer layer of cells with nodular thickenings; inner layer of cells with semiannular bands, the bands at times incomplete.

Spores verrucose, brown, 14–17 μm in diam. Elaters feebly tortuous to nearly straight, ca. 7.5–9 μm wide, bispiral.

Distribution and Ecology: Bipolar, in the Holarctic with a wide, Arctic–alpine distribution; in the Southern Hemisphere known from the southernmost tip of South America, South Georgia, Falkland Islands (Engel, 1990a), Antarctica, where "it is one of the most widespread and abundant of all Antarctic liverworts..." (Bednarek-Ochyra et al., 2000, p. 121) and New Zealand (South Island, 1065–1675 m).

Schuster (1968b, p. 486) stated "in New Zealand the species is restricted to the subalpine scrub zone or tussock zone, usually at elevations of 3500–5500 ft. Associated are several Holarctic taxa (*Anthelia juratzkana*, *Marsupella ustulata s. lat.*, *Cephaloziella arctica* subsp. *antarctica*, *Cephalozia bicuspidata s. lat.*) as well as *Schistochila splachnophylla*, *Lophozia autoica* and several other subantarctic taxa. Usually occurring over exposed, often broken soil, sometimes with *Polytrichum*." In the Old Man Ra. with *Hygrolembidium* at 1370 m (ca. 1 km N of summit of Shingle Creek Road, Otago); also over soil among tussocks with *Marsupella sprucei* and *Diplophyllum* cf. *dioicum* (Foggy Peak, Torlesse Ra., Canterbury, 1730 m).

Comments: The species has bifid leaves with thin-walled cells and minute to small trigones. The gemmae, typically present in New Zealand populations, are bright red and in exposed sites are copiously produced. This is the only one of our species with a ventral band of such smaller mycorrhizal cells in the stem. These cells, with maturity, become brownish and eventually, at least in part, disintegrate. The species is paroecious.

Subg. ***Isopaches*** (Buch) R.M.Schust.

Subg. *Isopaches* (Buch) R.M.Schust., Amer. Midl. Nat. 45: 56. 1951. Lectotype: *Lophozia bicrenata* (Schmid. *ex* Hoffm.) Dumort.

Lophozia pumicicola Berggr.

[Plate 12B]

Lophozia pumicicola Berggr., New Zealand Hepat. 21. *f. 15*. 1898. Type: New Zealand, North Is., near Lake Taupo, Jan. 1875, *Berggren* (G!).
Lophozia innominata E.A.Hodgs., Trans. & Proc. Roy. Soc. New Zealand 76: 69. 1946, *syn.*

fide Schuster (1968b, p. 472, 487). Type: New Zealand, South Is., Arthur's Pass, June 1942, *H. M. Hodgson & MacDonald* (MPN!).

Plants brittle, prostrate and firmly adhering to substrate, pale, whitish green, often reddish brown, the lobes often appearing bleached distally, the shoots minute, to 1 mm wide, 3 mm long, the shoots at times with only a few leaves. Stems firm, slender for shoot size, with cortical cells poorly differentiated, somewhat thick-walled, the exposed wall at times rather distinctly so, subequal to the medullary cells, a few ventral cells with mycorrhizal hyphae; medullary cells undifferentiated, ± uniform, with mycorrhizal hyphae present, at times in nearly all cells, the medulla becoming brownish with age (even when cortex is subpellucid). Rhizoids rather dense (even near shoot apices), scattered on ventral surface of stem, at times long for shoot size. Branches sparing, the shoots often simple, the branches of lateral-intercalary type. Leaves vertical, strongly dorsally assurgent and with much of leaf elevated above dorsal surface of stem, regularly homomallous, often closely imbricate, the insertion strongly succubous; leaves strongly concave, ovate, often rather broadly so, longer than broad or as wide as long, conspicuously narrowed in the apex, bifid to 0.25–0.35; lobes in flattened leaves often rather closely juxtaposed (the lobes often less than a third the maximal leaf width apart), ± parallel and non-divergent, acute, often apiculate, terminating in a single cell or a uniseriate row of 2 cells, the tip cell isodiametric grading up to 2× longer than wide, the lobes entire; sinus often sharply V-shaped; lamina margins rather evenly arched but the ventral margin a little dilated in basal half, the margins entire. Cells with walls thin, trigones medium and straight-sided, occasionally minute, the median cells 18–23 μm wide × 18–24 μm long (type) to 19–26 μm wide × 22–28 μm long; surface distinctly striate-papillose. Oil-bodies (Schuster, 2002a) 6–13 per cell, coarsely papillose. Underleaves typically absent, at times present, minute, linear to subulate. Asexual reproduction lacking.

Paroecious. ♂ Bracts in 1–2 pairs below the ♀ bracts; antheridia 1 per bract, the stalk uniseriate; paraphyses sometimes present among the antheridia, small, laciniiform. Gynoecia with bracts free from one another or distinctly connate dorsally, asymmetrically ovate, with apex and margins scarious, 2–3-lobed, the lobes entire or with 1–2 teeth; lamina margins entire or with 1–2 teeth below the middle; bracteoles connate on one or both sides for 0.25–0.4, at times connate on both sides and bracts also connate dorsally for ± the same distance, together forming a low, ensheathing tube, the bracteole small compared to bracts, undivided and subulate or short-bifid. Perianth relatively short, elliptic in outline, plicate distally, slightly contracted toward the mouth, the apex scarious, formed of guttulate, often distinctly hyaline cells, the mouth lobulate, the lobules irregularly dentate by teeth of 1–3, thick-walled cells.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (ca. 700–920 m), North Island (690–ca. 1200 m). Known from several scattered stations in New Zealand, including the central volcanic region of the North Island. The type occurred "growing on dry ground of gravel of pumice-stone amongst the common fern, *Pteris esculenta*" (Berggren, 1898, p. 21). In Tongariro Natl. Park at Mangatepopo Stream (below Soda Springs) on a thick soil layer over a boulder under low shrubby cover in an area of alpine vegetation with scattered frequent rocky outcrops. Schuster (2002a, fig. 300, p. 246) illustrated a plant from "frost flats near Minganui" (Taho Flats near Otupaka Stream, SW of Minginui). This site is an open, low area with scattered *Leptospermum scoparium* and *Dracophyllum subulatum* with abundant *Cladia retipora*. The species occurs there in a mossfield of *Polytrichum juniperinum*, *Campylopus clavatus*, *Chrysoblastella chilensis*, *Ditrichum punctulatum* and *Cladia aggregata*. Collec-

tions made by K. W. Allison in the 1930s suggest that the species was once common in the Rotorua–Kaingaroa area in similar situations. In the South Island (Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, Marlborough, ca. 700–920 m) over bare lichen-moss covered soil in rather open *Leptospermum scoparium* scrub in a serpentine area. Also beside the road north of Te Anau, Fiordland where among mosses in *L. scoparium* scrub and also at Arthur's Pass (type of *Lophozia innominata*). The ecology of the species needs further investigation based on the study of more collections, but the species is not an "ecological specialist, occurring apparently only on volcanic ash and known only from the central volcanic region of the North Island of New Zealand" as stated by Schuster (2002a, p. 247).

Comments: *Lophozia pumicicola* is a distinctive species. Plants are minute, with regularly homomallous, vertical, strongly dorsally assurgent, leaves with much of the leaf elevated above the dorsal surface of the stem. The leaves are strongly succubously inserted, often notably closely imbricate, strongly concave, bifid to 0.25–0.35, often rather broadly ovate and markedly narrowed at the apex, with the lobes often closely juxtaposed. Plants are paroecious, do not produce gemmae and underleaves are consistently lacking on sterile shoots. Also, the stem cortical cells are poorly differentiated, subequal to the medullary cells, which are undifferentiated, ± uniform and with mycorrhizal hyphae present.

The type of *Lophozia innominata* differs in some respects from the protologue of the species (Hodgson, 1946). Median leaf cells are 24–26 μm wide × 23–26 μm long and not "33–40" μm as stated by Hodgson (1946). Also, Hodgson (1946) stated the leaves are bifid or very rarely trifid. Sterile shoots of the type are consistently bilobed, but ♂ branches may have a sporadically trilobed leaf. The leaf surface is striate-papillose, although less conspicuously so than in other populations of the species, and trigones are medium and straight-sided. Hodgson (1946, p. 69) stated that the trigones are "parvis vel majusculis."

Lophozia bicrenata (Schmid. *ex* Hoffm.) Dumort.

Jungermannia bicrenata Schmid. *ex* Hoffm., [Schmid., Icon. Pl. Anal. Part. ed. 2. Manip. 3: 247. *tab. 64. f. 1*. Erlangen. 1796; *nom. inval.*], Deutschl. Fl. 2 (Addenda): "page" 38 (unpaginated), "after page 200." 1796 (1795) (*teste* Grolle, 1976). *Lophozia bicrenata* (Schmid.) Dumort., Recueil Observ. Jungerm. 17. 1835. *Isopaches bicrenatus* (Schmid.) Buch, Mem. Soc. Fauna Fl. Fennica 8: 288. 1933. Type (*fide* Grolle, 1976): (Germany) "Baden-Württemberg, Untersontheim bei Schwäbisch Hall, *leg.* Kemmler."

Plants stout and fleshy, closely attached to substrate, prostrate except for the ascending tips, green to reddish brown, odorous, shoots to 1 mm wide, to 10 mm long. Branching sparse, the shoots often simple. Stems thick and fleshy, the cortical cells similar to the medullary in diameter, somewhat thick-walled; medullary cells slightly less thick-walled or thin-walled, the ventral 2–3 cell layers (including the cortical) somewhat smaller in diameter and mycorrhizal with age. Rhizoids numerous, long, forming a dense mat to near shoot tips. Leaves somewhat dorsally assurgent, obliquely erect to erect-spreading, contiguous to moderately imbricate, somewhat to strongly concave, suborbicular-subquadrate to suboblate, averaging 1–1.2× as wide as long, bilobed to 0.25–0.3; lobes ± incurved, broadly acute to subacute, terminating in a single subisodiametric cell, the lobes entire or (rarely) with 1–2 isolated teeth; sinus crescentic or obtuse to rectangular. Cells thick-walled, usually strongly so, especially at the angles, the cell lumen often becoming guttulate, trigones indistinct, the median cells 22–27 μm wide × 30–34 μm long, the marginal cells ca. 19–24 μm diam.; surface smooth or faintly papil-

lose. Oil-bodies (Schuster, 1969c) in median sector of leaf (3)6–12(15) per cell, greyish, finely granular; oil-bodies absent in isolated or many cells of leaf margins and lobes, in other marginal and lobe cells small and inconspicuous, 2–6 per cell. Asexual reproduction by gemmae, the gemmae consistently and copiously produced, orange-red to reddish yellow to reddish brown, polygonal to stellate, 20–25 μm in diam., 1–2-celled, somewhat thick-walled and with thickened angles or protuberances; gemmiparous shoots not strongly ascending, with leaves becoming erose-lacerate with prolonged gemmae formation, but not smaller in size. Fungal partner a basidiomycete.

Paroecious (usually), at times heteroecious, with plants nearly always abundantly fertile and producing perianths and capsules throughout the growing season. Androecia below gynoecia, but at times isolated androecia on branches from below the gynoecia (then with small bracts); bracts of paroecious inflorescences imbricate, larger than leaves, somewhat concave, subequally bilobed with ventral lobe somewhat larger, the margins remotely and obscurely to distinctly finely dentate; antheridia 1–2 per bract, the stalk 1(2)-seriate. Gynoecia with bracts somewhat similar to the ♂ bracts immediately below except larger, bilobed or with 1–2 accessory lobes, the lobes typically distinctly dentate, rarely only remotely so; bracteole connate at base on one or both sides, lanceolate to obcuneate or oblong, sometimes shallowly 2–3-lobed, with a few scattered teeth. Perianth ca. 0.6–0.75 emergent, ovoid to cylindrical-ovoid, distinctly plicate in distal 0.5, narrowed to the mouth, the mouth often decolorate, spinose-dentate, the teeth acuminate, mostly 1–3 cells wide at base and 3–4 cells long, the terminal cell usually sharply tapering, 35–48 μm long, 3–5× as long as wide, the largest teeth often with 1–2 basal unicellular teeth; cells below mouth mostly hyaline, thick-walled.

Seta with ca. 16–21 rows of outer cells surrounding an inner core of 12–16 cells ± similar in size or somewhat larger. Capsule ovoid, the wall 2(locally 3)-stratose, the outer layer of cells subquadrate to short-rectangular, the radial walls with spine-like thickenings on longitudinal and transverse walls; inner layer of cells rectangular, with narrow, delicate band-like thickenings that usually extend 0.2–0.5 across the exposed tangential face, the bands at times extending farther as subcomplete or complete semiannular bands.

Spores 12–15 μm in diam., reddish brown, granulate-verruculose. Elaters ca. 8 μm wide, bispiral.

Distribution and Ecology: Circum-Laurasian + disjunct in southeastern Brazil (Gradstein and Pinheiro da Costa, 2003) and New Zealand: South Island (1940–1970 m).

In New Zealand known only from the alpine zone at the track to Gertrude Saddle, head of Gertrude Valley, Fiordland Natl. Park.

Comments: The species may be identified by the combination of the consistently 2-lobed, suborbicular-subquadrate to suboblate, contiguous to moderately imbricate leaves, the ± strongly, equally firm-walled cells, the consistent presence of copious orange-red gemmae, the normally ± strongly toothed ♀ bract lobes and the paroecious or heteroecious condition.

Tritomaria Schiffn. *ex* Loeske

Tritomaria Schiffn., Ber. Naturwiss.-Med. Vereins Innsbruck 31 (Beitrage): 12. 1908, *nom. inval.* Hedwigia 49: 13. 1909. *Sphenolobus* subg. *Tritomaria* (Schiffn.) Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland 6(1): 606. 1910.

Plants prostrate and with ascending apices to (with crowding) suberect to erect, pure green or brownish tinged or reddish or purplish brown or purplish black. Branching sparingly, the branches predominantly of *Frullania* type, at times of *Radula* type; lateral-intercalary branches present in some species; geotropic, microphyllous stolons and flagellae lacking. Stem with cortex firm, sometimes strongly thick-walled, in 1–2(3) strata; medulla dorsiventrally differentiated, the ventral strata of smaller cells that eventually become brown and mycorrhizal, the dorsal strata free of fungi. Rhizoids copiously produced, except sometimes toward shoot apices. Leaves vertically or subvertically oriented, widely spreading, the dorsal half of insertion transverse or inclined toward stem apex or (var. *novaezelandiae*) often becoming weakly succubous, the insertion extending to the stem midline dorsally and often decurrent; leaves dorsally assurgent, concave to canaliculate, typically (2)3(4)-lobed (in var. *novaezelandiae* 2–3-lobed, the 2- and 3-lobed leaves of about equal frequency), often asymmetrically so, with the third, dorsal lobe displaced basally and shorter than the 2 subequal ventral lobes; lobes sharp, at times cuspidate, entire (except *Tritomaria heterophylla*, where sometimes dentate), the apices at times becoming erose from gemmae formation; margins entire, never developing cilia at the base. Cells with walls firm, the median cells with trigones usually bulging; median and basal cells away from marginal sectors often conspicuously elongated; surface weakly to distinctly papillose or (in ours) striate throughout. Oil-bodies (Schuster, 2002a) medium-large, usually 4 or more per cell, finely botryoidal or granular-botryoidal. Underleaves absent; ventral merophytes obsolete, at most 2 cells broad. Asexual reproduction by gemmae rare to ubiquitous, the gemmae yellowish brown to golden to reddish brown or red, elliptical or polygonal, 2-celled at maturity.

Dioecious. Androecia intercalary, the bracts leaf-like except concave to moderately ventricose at base; antheridia usually 2–4 per bract, the stalk 1- or 2-seriate. Gynoecial bracts usually nearly leaf-like and commonly lobed like the leaves or with 1–2 accessory lobes, often broader or sometimes (*Tritomaria heterophylla*) ciliate-dentate; bracteole absent or (at least in *T. scitula*) narrow, oblong, connate for most of its length with 1 bract. Perianth cylindrical-obovoid, rather deeply plicate above the middle, gradually contracted to the mouth, the mouth considerably (subg. *Tritomaria*) or hardly so (subg. *Saccobasis*), the mouth entire or dentate-ciliate.

Seta of numerous cells, unspecialized. Capsule wall 3–5-stratose; outer layer of cells with nodular thickenings; inner layer of cells with semiannular bands.

Lectotype (Kitagawa, 1966): *Tritomaria exsecta* (Schmid. *ex* Schrad.) Loeske (≡ *Jungermannia exsecta* Schmid.)

A basically Laurasian genus with some eight species belonging to three subgenera; for details of the distribution of the species see Engel (2006a). One species is bipolar and occurs in our area.

The generic description is adapted and modified from Schuster (1969b).

References: Engel (2006a); Kitagawa (1966); Schuster (1969b, 2002a).

Tritomaria exsecta (Schrad.) Loeske

Jungermannia exsecta Schmid. *ex* Schrad., Syst. Samml. Kryptog. Gew. 2: 5. 1797; Schmid., Icon. Pl. Anal. Part. ed. 2, Manip. 3: 241. tab. 62, 1796, *nom. inval. Lophozia exsecta* (Schmid. *ex* Schrad.) Dumort., Recueil Observ. Jungerm. 17. 1835. *Scapania exsecta* (Schmid. *ex* Schrad.)

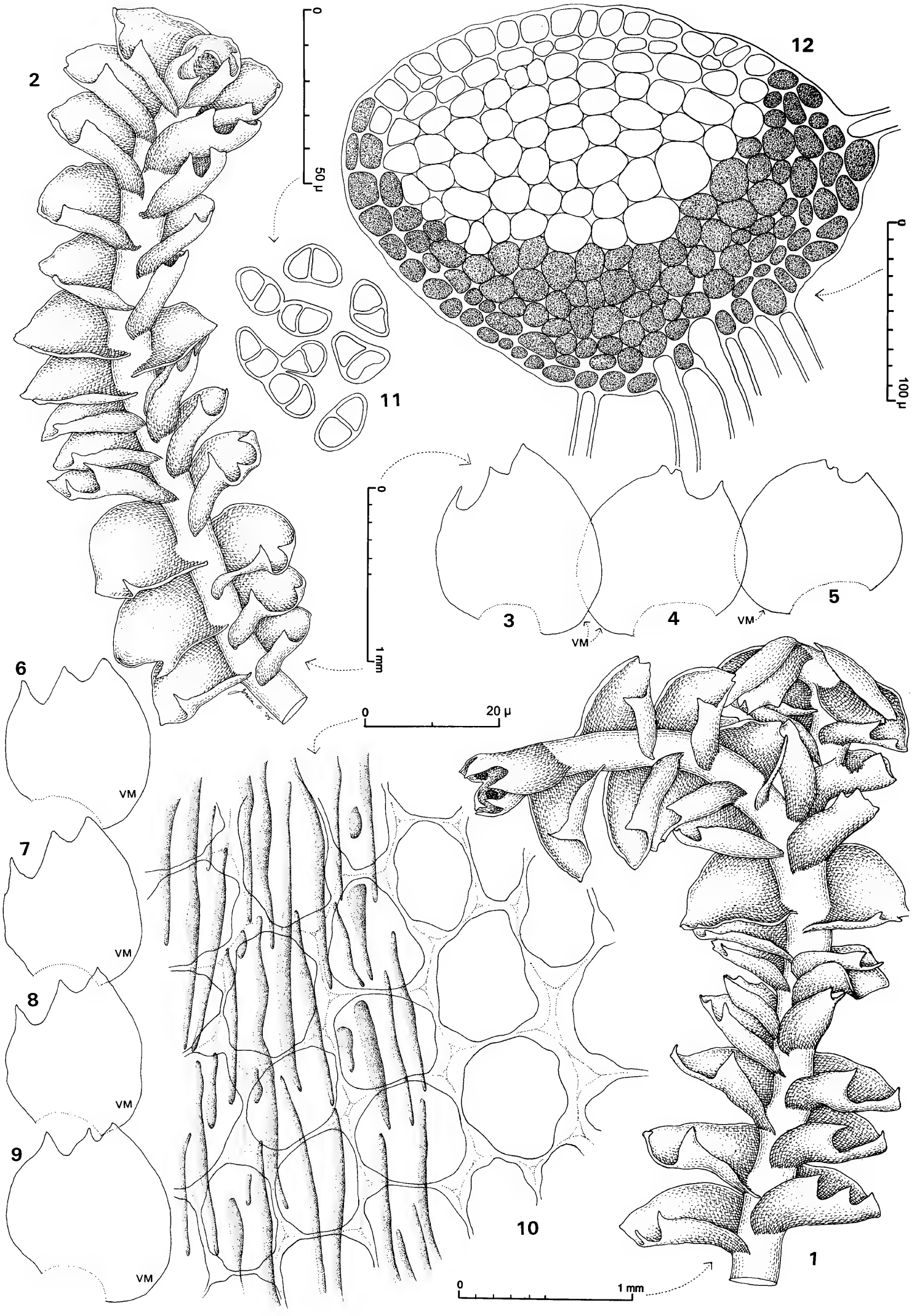

Fig. 144.
Tritomaria exsecta (Schrad.) Loeske subsp. *novaezelandiae* J.J.Engel. 1. Leading shoot with *Frullania*-type branch, dorsal view; gemmae are present at apex of both main shoot and branch, the young leaves of the branch tip cover the cluster of gemmae. 2. Leading shoot, dorsal view; note

Austin, Hepat. Bor.-Amer. Exsicc. 8(21). 1873. *Diplophyllum exsectum* (Schmid. *ex* Schrad.) Thériot & Monguillon, Bull. Soc. Agr. Sci., Le Mans 1899: 199. 1899. *Sphenolobus exsectus* (Schmid. *ex* Schrad.) Steph., Sp. Hepat. 2: 170. 1902. *Tritomaria exsecta* (Schmid. *ex* Schrad.) Schiffn. *ex* Loeske, Hedwigia 49: 13. 1909; Schiffn., Ber. Naturwiss.-Med. Vereins Innsbruck 31 (Beitrage): 12. 1908, *nom. inval.* Type: Germania, Bavaria.

Engel (2006a) subdivided the species into two subspecies, subsp. *exsecta* and subsp. *novaezelandiae*; only subsp. *novaezelandiae* occurs in our area.

Tritomaria exsecta (Schrad.) Loeske subsp. ***novaezelandiae*** J.J.Engel

[Figs. 144, 145]

Tritomaria exsecta (Schrad.) Loeske subsp. *novaezelandiae* Engel, Bryologist 109: 61. *f. 1, 2.* 2006. Holotype: New Zealand, South Is., Nelson Prov., St. Arnaud Ra., Rainbow Skifield just below skitow area, E of S end of Lake Rotoiti, S of St. Arnaud, 1210 m, *Engel 22800* (F); isotype: (CHR).

Plants rather stiff, brittle (both stems and leaves), loosely creeping, the distal sector of shoots stiffly ascending, the shoot apices distinctly and sharply curved upward, the plants pale green, at times tinged with pale brown, medium in size, to 1.5 mm wide. Branching sparing, irregular, the branches lateral-intercalary, from the median sector of leaf axils; *Frullania*-type branches present, occasional. Stems rather stout for plant size, the cortex in 2–3 rows of firm-walled, smaller cells, the cortical cells in ventral half of stem with mycorrhizal infection, with exposed wall distinctly thickened and orange-brown; medullary cells thin-walled, differentiated dorsiventrally, the ventral layers of small cells strongly mycorrhizal, the dorsal layers of large cells lacking fungi. Rhizoids frequent, even at shoot apex, rather short for plant size, scattered, but with a tendency for formation of fascicles at ventral leaf bases, the rhizoids reddish brown toward bases, colorless distally. Leaves rigid, strongly dorsally assurgent, the entire leaf widely spreading or the ventral half of leaf (+ ventral-most lobe) widely spreading and the dorsal sector incurved and becoming suberect, the leaves then weakly conduplicate (but never with a sharp keel or fold), the leaves approximate to loosely imbricate, strongly succubously oriented (appearing weakly succubously oriented when dorsal margin suberect), the insertion strongly succubous for most of its length, often becoming weakly succubous to subtransverse at dorsal end; leaves rather strongly concave, suborbicular to oblate, often asymmetric and then with the ventral sector somewhat dilated resulting in the ventral margin becoming distinctly longer, the leaves 665–805 μm wide × 575–630 μm long to 775–980 μm wide × 700–915 μm long, 1.05–1.5× wider than long, shallowly 2–3-lobed to 0.1–0.2, the lobe number variable, inconsistent, the 2- and 3-lobed leaves of about equal frequency, the lobing at times asymmetric, the ventral lobe somewhat larger, with continued gemmae production the lobe apices becoming increasingly erose, irregular, and the lobe number obscured, at times the leaf apices even appearing undivided and obtuse; lobes (lacking gemmae formation) medium to rather broadly acute, terminating in a single cell or a uniseriate row of 2 cells, the tip cells

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variation in leaf form, especially the apices, and the presence of gemmae at the shoot apex. 3–9. Leaves, note variation in shape and lobing (VM = ventral margin). 10. Median leaf cells, the striations of leaf surface shown at left. 11. Gemmae. 12. Stem, cross section. (All from type.)

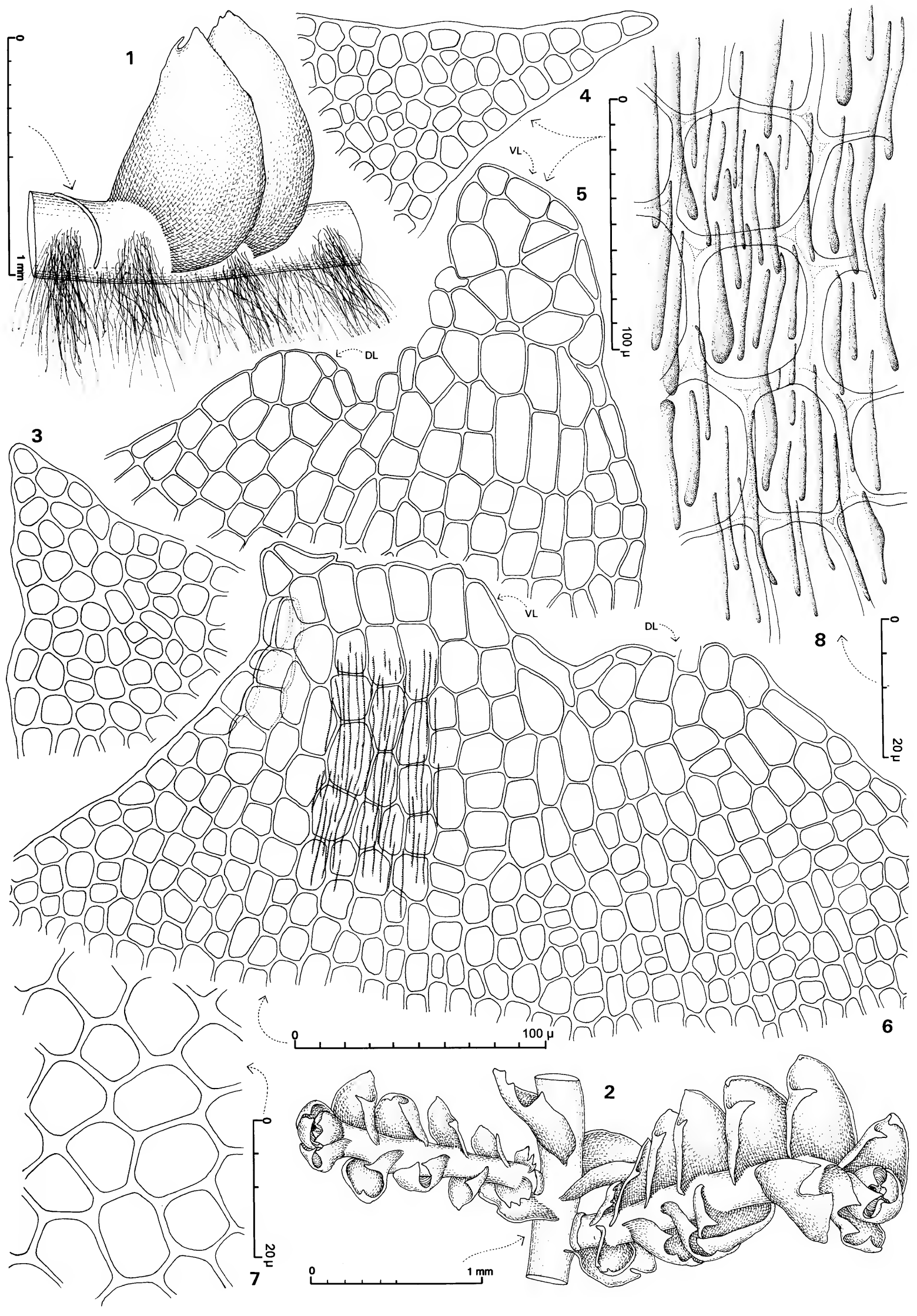

Fig. 145.
Tritomaria exsecta (Schrad.) Loeske subsp. *novaezelandiae* J.J.Engel. 1. Leading shoot, lateral view; note succubous insertion and distribution of rhizoids, including from lateral sides of stem. 2.

± isodiametric, the lobes at times terminating in a pair of laterally juxtaposed cells, the lobe margins entire; sinuses ± narrowly rounded; lamina margins entire, the dorsal strongly and broadly arched, narrowing toward the base, the ventral margin arched similarly to the dorsal or, more often, more strongly so, subcordate at the base. Cells in median sector of leaf thin-walled, trigones distinct, straight-sided to slightly bulging, the median cells very small, subisodiametric, 11–14 μm wide and long; cells toward apex, margins and base evenly thick-walled, with trigones absent or small and concave-sided; median basal cells somewhat larger, 12–18 μm wide × 20–25 μm long; surface striate throughout, even at leaf apex, the median cells with 2–5 striae per cell, some extending the length of 2–4 cells. Underleaves (even rudimentary) totally lacking. Asexual reproduction by gemmae, the gemmae copiously produced, reddish brown, basically smooth, broadly elliptic, often irregularly so, often attached to one another in groups of 2 or 3, the gemmae 2-celled, 10.1–11 × 16.3–17.3 μm; gemmiparous shoots not strongly ascending, the leaves with prolonged gemmae formation not smaller in size. Fungal partner a basidiomycete.

Androecia and gynoecia unknown.

Distribution and Ecology: *Tritomaria exsecta* is bipolar (see Engel, 2006a). Subspecies *exsecta* is widespread and common in virtually the entire temperate/subarctic sectors of Laurasia, in the New World occurring south to Mexico (2000–3000 m), in Africa known from the high volcanoes of East Africa, the Sani Pass (Natal) on the border with South Africa, and Ethiopia (for details see Engel, 2006a).

Subspecies *novaezelandiae* is known only from the type, which was found growing over rock of a vertical cliff face in a steep-sided, narrow stream valley with nearly vertical cliff-like sides in a *Nothofagus solandri* var. *cliffortioides* forest.

Comments: *Tritomaria exsecta* subsp. *novaezelandiae* may be recognized by several characters. Plants are pale green and develop brownish pigmentation, and the branches are of the lateral-intercalary and *Frullania* types (Fig. 144: 1; Fig. 145: 2). The leaves are 2–3-lobed, with lobe number in about equal frequency (Fig. 144: 1, 3–9), and the dorsal lobe is always smaller. The leaves are notably concave (Fig. 144: 1, 2; Fig. 145: 1, 2), and the leaf insertion is succubously oblique for most of its length, but transverse to subtransverse to weakly succubous at the dorsal third (Fig. 144: 1, 2; Fig. 145: 2). Areolation is distinctive: leaf cells are small, subisodiametric and only 11–14 μm wide and long, with well-developed trigones, but the cells toward the apex, margins and base tend to be evenly thick-walled, with trigones absent or somewhat developed (Fig. 145: 3, 4, 6). The leaf surface is distinctly striate throughout, i.e., even toward the leaf apex (Fig. 145: 6, 8). Reddish brown gemmae are copiously produced and are basically smooth, broadly elliptic and 2-celled (Fig. 144: 11). Stem medullary cells are dorsiventrally differentiated with strong mycorrhizal infection (Fig. 144: 12).

Leading shoot with 2 lateral-intercalary branches, dorsal view (gemmae are present at the tips of both branches). 3, 4. Leaf lobes without gemmae formation (both drawn to same scale). 5, 6. Distal sectors of leaves involved with gemmae formation (DL = dorsal lobe; VL = ventral lobe), note that distal cells are larger, the striae indicated in part in fig. 6. 7. Intramarginal cells in dorsal-basal third of leaf. 8. Median-basal cells of leaf showing surface striae (lower = leaf base). (All from type.)

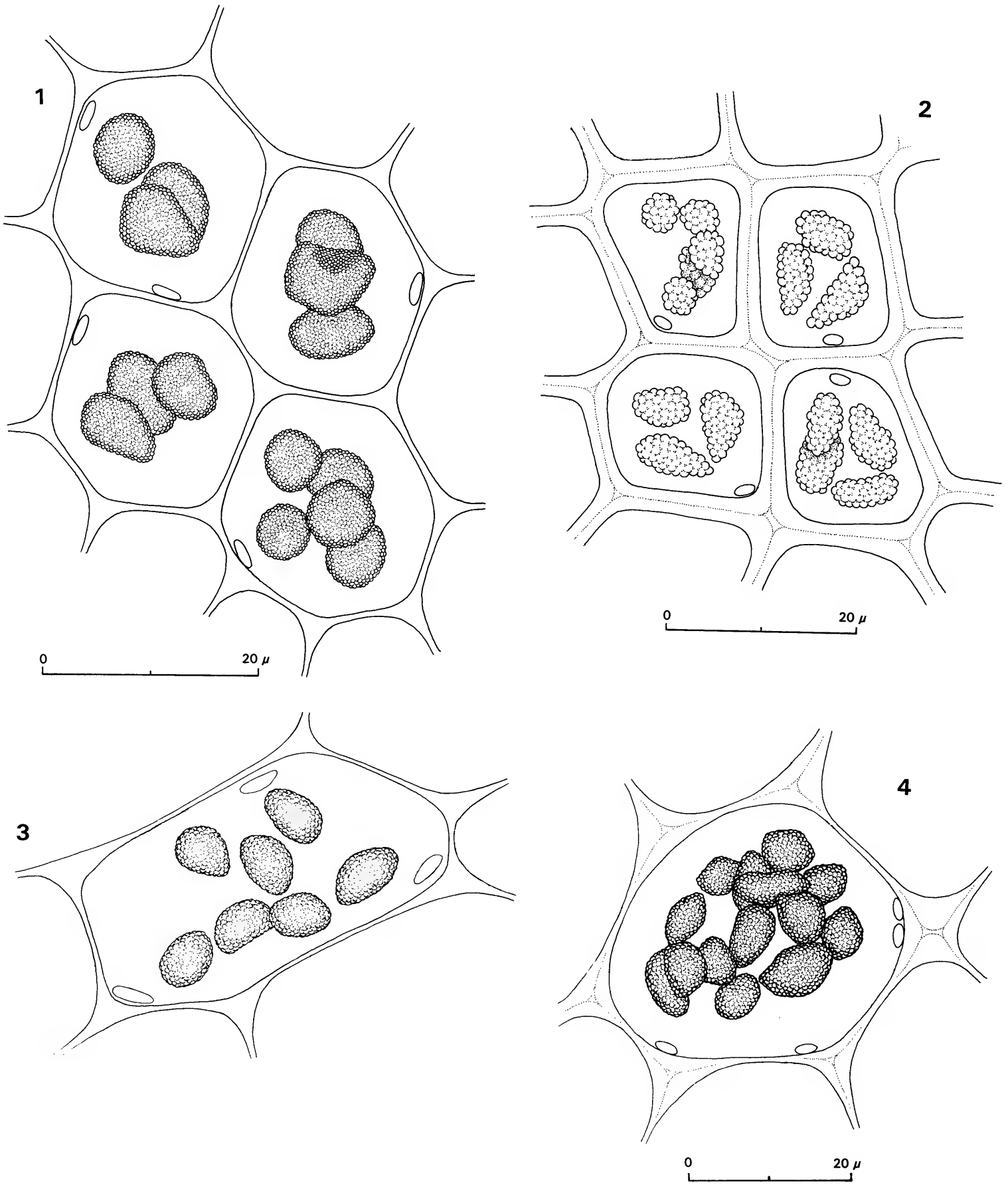

Fig. 146.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Adelanthus gemmiparus* (R.M.Schust.) E.A.Hodgs. Median leaf cells. 2. *Adelanthus occlusus* (Hook.f. & Taylor) Carrington. Median leaf cells. 3. *Lophozia autoica* R.M.Schust. Median lamina cells. 4. *Lophozia* cf. *monoica* (E.A.Hodgs.) J.J.Engel. Median lamina cells. (Fig. 1, from *Engel 26952*, New Zealand, North Is., Tongariro Natl. Park, Falls Track, off Ohakune Mtn. Road; 2, from *Engel 27075*, New Zealand, South Is., Western Nelson EP, Kahurangi Natl. Park, Matiri Ra., Thousand Acres Plateau; 3, from *Glenny 9116*, New Zealand, South Is., Westland EP, Mt. Brown; 4, from *Glenny 9110*, New Zealand, South Is., Westland EP, Mt. Brown.)

Anastrophyllum (Spruce) Steph.

Anastrophyllum (Spruce) Steph., Hedwigia 32: 139. 1893. *Jungermannia* subg. *Anastrophyllum* Spruce, J. Bot. 15: 235. 1876.

Plants usually rather rigid, ascending to erect, especially if gemmae are formed, typically red to reddish brown to ± fuscous (even in shade), rarely deep green when in dense shade; minute and less than 500 μm wide to vigorous and to 3.5 mm or more wide; leafy shoots never becoming microphyllous and flagelliform distally. Branching sparingly, usually from lower sectors of shoots, the branches variable, at times lateral-intercalary, from middle or ventral ends of leaf axil; *Frullania* or *Radula* types sometimes present; dorsal-intercalary (*Andrewsianthus*-type) branching absent; geotropic, microphyllous, rhizoidous axes rare. Leaves firm, alternate, vertically oriented, the dorsal end of insertion transverse, extending to stem midline, often decurrent along dorsal midline of stem, the ventral half of insertion succubous (at very end of insertion again transverse or weakly decurrent), the leaves strongly concave, usually concave-canaliculate, the leaves bifid usually to 0.2–0.65; lobes acute to acuminate, rarely obtuse, the apices often somewhat incurved, the margins entire. Cells with large to coarsely nodose trigones that are confluent or separated by narrow thin-walled places (pits), the cell lumen often bounded mostly by the massive trigones, the cell walls sometimes uniformly thick-walled; cells in lobes and marginal sectors of lamina subisodiametric, those in a basal-median field usually conspicuously elongated, often 2–3:1; surface smooth or weakly (rarely strongly) papillose. Oil-bodies present in all cells, 3–4 per cell, granular to papillose, rather small. Underleaves lacking, sometimes even in gynoecial regions. Asexual reproduction usually lacking, at times present and by gemmae, the gemmae angular, formed at tips of upper leaves, sometimes on erect flagelliform shoots.

Dioecious (autoecious and paroecious in the Arctic *Anastrophyllum sphenoloboides*). Androecia ± spicate, the bracts ventricose at the base, the dorsal margin often with a distinct tooth toward the base; antheridia usually 1–2 per bract, the stalk 1–2-seriate; paraphyses absent. Gynoecial bracts usually bifid and similar to leaves except larger; bracteoles absent or present, free or connate on one side, unlobed, tapered to the summit. Perianths long-emergent, terete below, deeply plicate in distal sector, some taxa 3-plicate and with the dorsal face with a sulcus, some taxa pluriplicate, the perianths contracted toward the usually ciliate-dentate to ciliate-lanceolate, commonly bleached mouth.

Seta usually of the general type, some taxa (subg. *Crossocalyx*) with 8(9) rows of outer cells and 4(5) rows of inner cells. Capsule wall usually 3–5-stratose, less often 2- or 2–3-stratose; outer layer of cells with nodular thickenings; inner layer of cells with semiannular bands, the bands often thin or incomplete on middle of tangential walls.

Spores papillose-short-vermiculate, spore:elater diam. ratio ca. 2:1.

Lectotype (Schuster, 1961b): *Anastrophyllum donianum* (Hook.) Steph. (≡ *Jungermannia doniana* Hook.)

One of the two largest genera in subfamily *Lophozioideae* (the other is *Lophozia*). We are accepting the broad delimitation given the genus *Anastrophyllum* by Schuster (1951, 1953, 1969c, 2002a), where the *Sphenolobus*, *Crossocalyx* and *Eremonotus* complexes are included within *Anastrophyllum*. *Anastrophyllum* contains ca. 30–35 species (Schuster, 2002a), but we note that Váňa (1984, p. 100) concludes, after further study, that there may be more (probably 35–40) species.

The genus *Anastrophyllum* has a broad range that includes both Arctic and south temperate species, but is concentrated in tropical-montane areas. Gradstein et al. (2001, p. 110), for example, stated that ca. 10 species occur at high elevations in tropical America and "*Anastrophyllum* is one of the most characteristic genera of the páramo." Ten species are known from the south temperate–subantarctic zone. Extra-New Zealand species are:

1) *Anastrophyllum auritum* (Lehm.) Steph. (type: South Africa, Table Mtn.) is pantropical. In Latin America a Cordilleran species that ranges from Mexico to Tierra del Fuego (Váňa, 1984); South Africa, Cape Prov. (Arnell, 1963; Váňa, 1982); Crozet Island (Grolle, 1971a); Marion Island (Grolle, 1971b). Váňa (1984, p. 102) states "this species, which is extremely variable ... has been described under many names (until now known as *A. leucostomum* (Taylor) Steph.)."
2) *Anastrophyllum ciliatum* Steph. occurs on South Georgia, Falkland Islands and the southern Magellanian region (see Engel, 1978, 1990a).
3) *Anastrophyllum crebrifolium* (Hook.f. & Taylor) Steph. (lectotype [*fide* Engel, 1978]: Chile, Prov. Magellanes, Cabo de Hornos, *Hooker* [FH!]); syn.: *Anastrophyllum leucocephalum* (Taylor) Steph. (type: Ecuador, Volcan Cayambe, 4265 m, *Jameson* [FH!, NY!]). The species occurs in southern South America (Tierra del Fuego, Patagonian Channel region), Juan Fernandez, higher elevations in Andes of Peru and Ecuador. See remarks in Engel and Braggins (1998).
4) *Anastrophyllum involutifolium* (Mont.) Steph. (syn.: *Anastrophyllum decurvifolium* (Sull.) Steph.) of southern South America (Tierra del Fuego, southern Patagonian Channel region) and Juan Fernandez (see Engel, 1978).
5) *Anastrophyllum minutum* (Schreb. *ex* Cranz) R.M.Schust. (type: Greenland) is a broadly distributed Holarctic species (cf. Schuster, 1969c) and occurs in the Southern Hemisphere as a disjunct at high elevations in New Guinea and South Africa (Arnell, 1963 as *Sphenolobus minutus* (Schreb. *ex* Cranz) Steph.; Váňa, 1982). Reported from Kerguelen by Hooker and Taylor (1844a) and Gottsche et al. (1844–47); the record is probably erroneous (Váňa, 1982).
6) *Anastrophyllum piligerum* (Nees) Spruce (type: Java), syn.: *Anastrophyllum incumbens* (Lehm. & Lindenb.) Steph. (type: Tristan da Cunha). A pantropical species, including presence in Zimbabwe on Inyanga Mtn., and Tristan da Cunha (Váňa, 1982, 1984).
7) *Anastrophyllum tristanianum* J.J.Engel is endemic to Tristan da Cunha (see also comments in Engel and Braggins, 1998).

The generic description after Schuster (2002a) but modified.

References: Engel and Braggins (1998); Schuster (1966c, 2002a).

Key to Species

1a. Plants rather robust, to 1800 μm wide; leaves strongly dorsally falcate-secund, asymmetric, broadly overlapping dorsally and extending across stem and somewhat beyond; leaf margins smooth and entire, sometimes weakly crenulate or distantly toothed; antheridia 2–3 per bract, the stalk biseriate; oil-bodies 2–3 per cell; plants of open areas in forests above ca. 430 m and penalpine zone . . . . . *A. schismoides* (p. 675)

1b. Plants minute, to 800 μm wide; leaves widely spreading, not dorsally secund, ± symmetrical, distant to at most loosely imbricate and dorsally not extending across or beyond stem; leaf margins distinctly crenulate (at least in distal half of leaf) by dilated, projecting, anticlinal walls of the marginal cells; antheridia 1 per bract, the stalk uniseriate; oil-bodies 3–6 to 4–8 per cell; plants of alpine zone 2

2a. Leaf surface smooth; branching strictly terminal, *Frullania* type; basal cells of leaf elongated, commonly ca. 2:1; oil-bodies nearly homogeneous, the lobe cells with 0–1 oil-bodies per marginal cell and 4–8 oil-bodies in intramarginal lobe cells . . . . . *A. novazelandiae* (p. 680)

2b. Leaf surface strongly striate-papillose; branching nearly always lateral-intercalary; basal cells of leaf not or hardly elongated, usually 1–1.7:1, rarely ca. 2:1; oil-bodies finely granular, similar in number (3–5) in all lobe cells . . . . *A. papillosum* (p. 681)

Anastrophyllum schismoides (Mont.) Steph.

[Plate 13C; Figs. 147, 148; Fig. 150: 1, 2, oil-bodies, p. 684]

Jungermannia schismoides Mont., Ann. Sci. Nat. II. 19: 250. 1843. *Anastrophyllum schismoides* (Mont.) Steph., Hedwigia 32: 140. 1893. Original material: Auckland Is., *Hombron*.

Plants suberect to erect, yellow-brown to reddish brown to deep red to wine-red, the shoot tip dorsally hooked to subcircinate; shoots rather robust, to 1.8 mm wide. Branching rather frequent, of lateral-intercalary type; leafless lateral-intercalary stolons rather common, slender, wire-like, with rhizoids. Stems rather rigid, the cortex with outermost layer of cells with moderately and evenly thickened walls, the subepidermal 2–3 layers distinctly thick-walled and deeply pigmented; medullary cells thin-walled, colorless. Rhizoids not seen on leafy shoots. Leaves rigid, strongly dorsally falcate-secund, the dorsal half of leaf lamina (in dorsal view) ± vertically oriented, the opposing leaves loosely and broadly overlapping dorsally and extending across the width of stem and often somewhat beyond, the dorsal lobe incurved to spreading to squarrose-reflexed, the ventral lobe usually broadly channeled and incurved; leaf bases (in ventral view) tightly shingled and appressed to the stem, the shoots in ventral aspect strongly convex; insertion transverse in dorsal half and extending to stem midline dorsally, obliquely succubous in ventral half; leaves deeply channeled, when flattened broadly elliptic to oblate-ovate to subreniform, with a subcordate base, (1200)1600–1800 μm wide × (800)1100–1800 μm long, ± asymmetrically shallowly to distinctly bilobed to 0.3–0.45, the dorsal lobe usually smaller and narrower than the ventral, the sinus base acute to broadly U-shaped; lobes entire or obscurely and distantly toothed, the lobes broadly to narrowly acute, terminating in a single sharp cell or more commonly the lobe tips slenderly acuminate, often apiculate, often hyaline, terminating in a uniseriate row of 2–6(7) ± isodiametric or at most moderately elongated cells; dorsal margin of lamina entire to obscurely crenulate by projecting septa, or distantly toothed by blunt to rather narrow, sharp teeth, the margin moderately arched, contracted at the base, not decurrent; ventral margin broadly ampliate, contracted to a subcordate base, not decurrent. Cells in median portion of leaf thin-walled, with bulging to nodulose, often confluent trigones, the lumen ± stellate, the cells 14–18 μm wide × 19–22 μm long, the basal cells often deeper pigmented (often red-brown), somewhat larger, but not much elongated; marginal cells of leaves at times weakly longitudinally elongated, lacking trigones (the free wall thickened), forming an indistinct border, the margin sometimes weakly crenulate by projecting septa of the marginal cells; surface rather obscurely striate-papillose, becoming

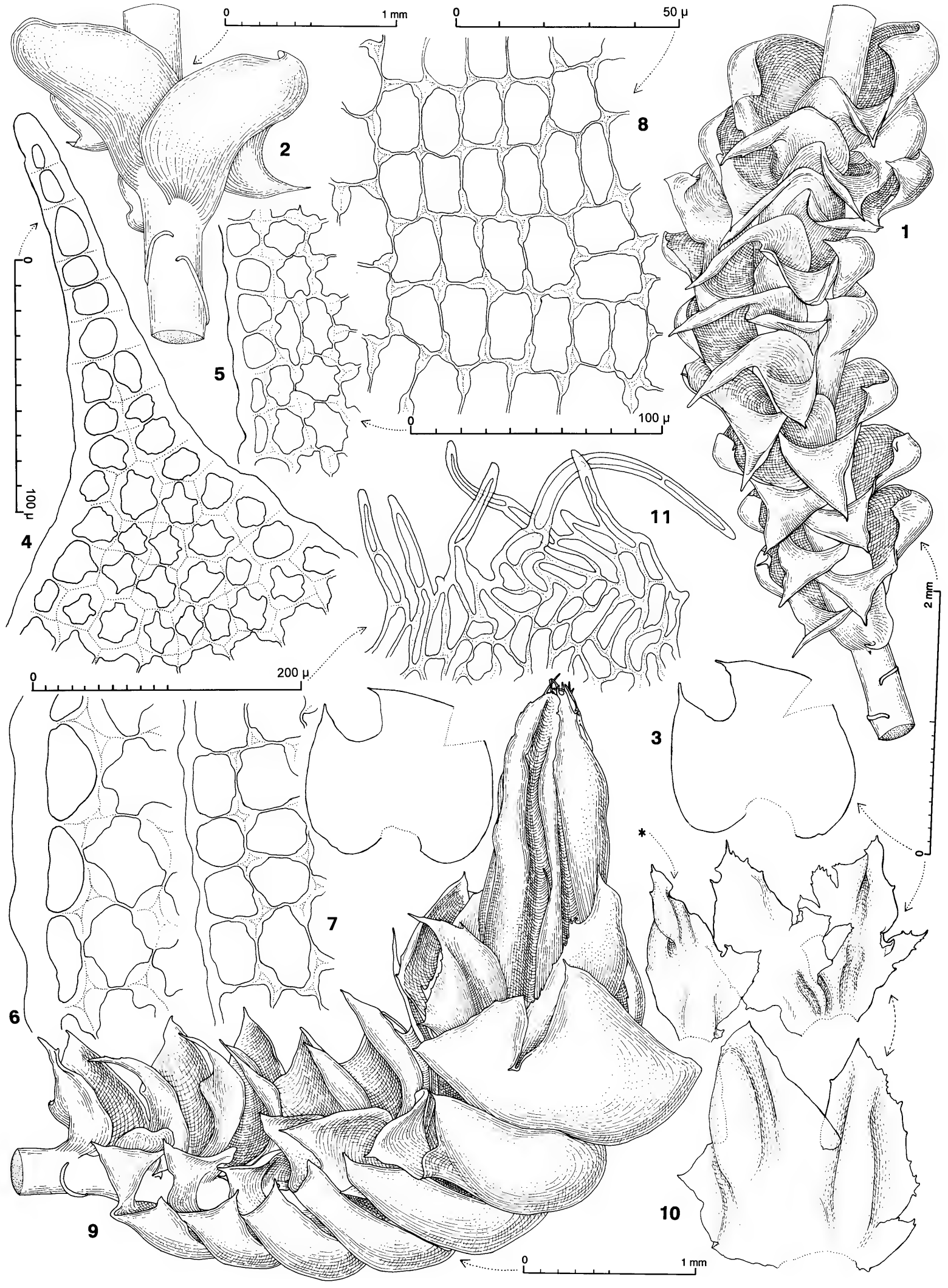

Fig. 147.
Anastrophyllum schismoides (Mont.) Steph. (figs. 1–6, 9–11, var. *schismoides*; 7, 8, var. *crassulum*). 1. Portion of shoot with sterile sector (basal) and (distally) the basal sector of androecium, dorsal view (note androecium wider than sterile sector). 2. Leaf pair (note leaf insertion), ventral view. 3. Leaves (to left and right of perianth). 4. Leaf lobe (distal sector). 5. Dorsal margin of lam-

distinctly long-striate toward leaf base. Oil-bodies pale smokey grey, opaque, in lamina middle 2–3(4) to (2)3–5 per cell, moderately papillose, the globules moderately protruding beyond membrane, the oil-bodies subglobose to elliptic, often rather broadly so, at times irregular in shape, most 3.8–5.8 × 6.7–7.7 μm, some 4.3–4.8 × 4.8–5.3 μm; basal cells each with 3–5 oil-bodies per cell. Underleaves absent. Gemmae rather common, 2-celled, pale, 18.2–18.7 μm in diam., polygonal, typically with 6 blunt projections. Fungal partner absent.

Dioecious. Androecia becoming intercalary on main shoots or long branches, a little wider than vegetative sectors (often recognizable only by the inflated bases of the bracts), with up to 5 pairs of bracts; bracts of similar size to leaves, deeply concave to subcupulate at base with a broad, convex bulge, the dorsal margin weakly undulate, entire to obscurely crenate, usually with a lobuliform tooth at the base; antheridia 2–3 per bract, the stalk biseriate; paraphyllia sporadically present, irregular and lobe-like, inserted on median dorsal surface of stem or in axil of bract. Gynoecia on main shoots and leading lateral-intercalary branches, in absence of fertilization often with a single, strong subfloral innovation continuing growth of the shoot; outer involucral bracts slightly to at most moderately larger than leaves, straight, not falcate, closely imbricate, deeply concave, asymmetrically bifid; innermost pair of bracts somewhat smaller, often ± plicate, at times ± symmetrically bifid to 0.5, the lobes often with a few minute teeth, the sinus at times broadly dilated, reflexed and with irregular lobuliform extensions, the lamina margins each with a lobule and minute accessory teeth; a third scale-like bract sometimes present, ca. 0.5 or even 0.25 the size of innermost pair of bracts, irregularly 2–3-lobed, inserted at perianth base or some distance above the base; bracteoles absent. Perianth narrowly elliptic to fusiform, tapering gradually to the mouth, deeply plicate in distal 0.5–0.75, at times with a few broad plicae descending almost to the perianth base; mouth shallowly lobulate, the lobules acute, irregularly ciliate and toothed, the lobule margins with sharp, projecting teeth and short, flexuous cilia, the cilia uniseriate, of 2–4 elongated cells; lobules of mouth sharply distinct in areolation, the cells contorted and sinuous, with evenly thickened walls, the cells of the perianth proper similar to those of the leaves; perianth 4–5-stratose in basal sector.

Seta 14–15 cells in diam., with 45–48 rows of outer cells surrounding an inner core of somewhat smaller cells. Capsule short-ellipsoidal, the walls 53–56 μm thick, of 4–5 layers, the outer layer of cells equal to thickness of ca. 1.9 of interior strata; outer layer of cells with distinct one-phase development, the cells subquadrate to short-subrectangular, with red-brown nodule-like to spine-like thickenings on both longitudinal and transverse walls; semiannular bands occasionally present but usually only 1(2) per cell, and typically at the cell ends, the thickenings at times anastomosing, particularly at the cell corners, but without development of fenestrae; inner layer of cells subrectangular, semiannular bands common, rather closely spaced, the bands often non-pigmented in median portion, often incomplete, the radial walls

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ina. 6, 7. Margins in distal sector of leaf lamina, the exposed wall of marginal cells in fig. 6 is hyaline (both figs. drawn at same scale as fig. 8). 8. Cells toward base of lobe. 9. Shoot with gynoecium, dorsal-lateral view. 10. Innermost ♀ bracts (at arrows) and (upper left, at *) a smaller scale-like bract. 11. Perianth mouth. (Figs. 1, 2, from *Engel 17959*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, summit area of Haast Pass; 3–5, from *Engel 21978*, New Zealand, South Is., Fiordland EP, head of Gertrude Valley; 6, from *Engel 12834*, Tasmania, Hartz Mountains Natl. Park, summit of Devils Backbone; 7, 8, from type of var. *crassulum*; 9–11, from *Hatcher 693*, New Zealand, South Is., Fiordland EP, trail between Gunn's Camp and Hidden Falls.)

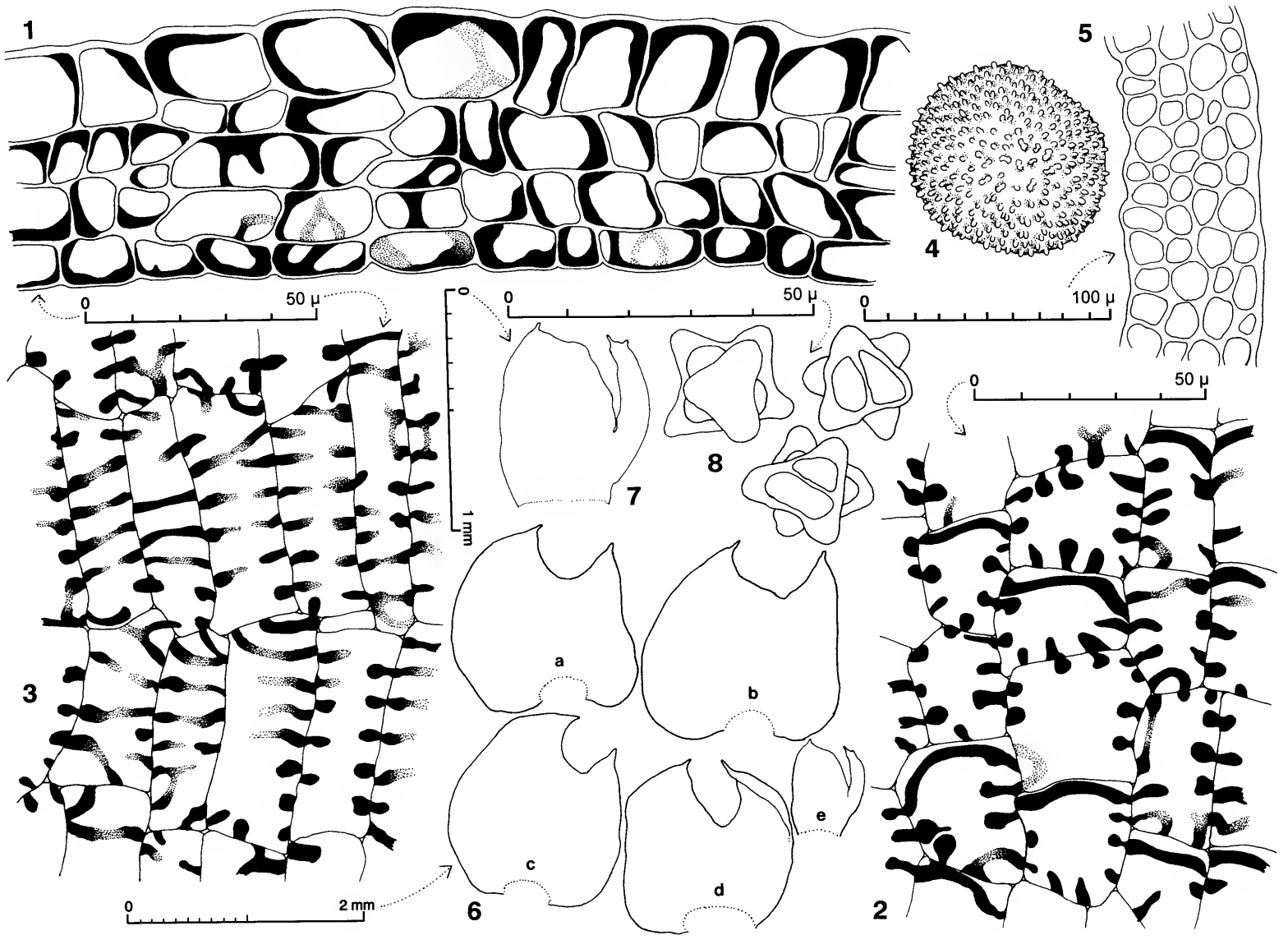

Fig. 148.

Anastrophyllum schismoides (Mont.) Steph. 1. Capsule wall, cross section. 2. Capsule wall, outer layer. 3. Capsule wall, inner layer. 4. Spore (× 1760). 5. Perianth base, cross section. 6. Subinvolucral + involucral bracts from one side of axis, consecutive sequence from outer (= a) to innermost (= e, which is also shown at higher mag. in fig. 7). 7. Innermost ♀ bract (inserted on lower sector of perianth). 8. Gemmae. (Fig. 8, from *Engel 15134*, Tasmania, Sentinel Ra., between Lakes Gordon and Pedder; remainder from *Cameron 757J*, New Zealand, North Is., Auckland EP, Coromandel Ra., SE of Mt. Moehau.)

often with nodule-like to spine-like thickenings, the bands or thickenings occasionally forking and anastomosing but at best delimiting only isolated fenestrae.

Spores 11–13 µm in diam., red-brown, with rather sharply defined, rather large papillae that sporadically coalesce to form at most short-vermiculate features. Elaters slightly tortuous to nearly straight, 6.7–8.2 µm wide, bispiral to tips, the spirals 1.9–2.4 µm wide, reddish brown.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands, Antipodes Islands, Stewart Island (330–530 m), South Island (20–1310 m), North Island (740–960 m), Chatham Islands. Otherwise amphi-Pacific-temperate: Australia: Tasmania, Victoria; southern South America. In New Zealand known from Fiordland, Southland, Otago, Westland, Canterbury (near the Main Divide), Western Nelson, Southern North Island (Tararua Ra.), Volcanic Plateau (Rainbow Mtn.), Taranaki (Pouakai Ra.) and Auckland (Mt. Moehau) EPs. Most abundant in Westland, Otago and Southland.

In New Zealand the species often forms large, usually pure populations, mostly occurring above ca. 430 m and into the penalpine zone. The species is shade-intolerant, and in forested areas it is found where there is considerable exposure to light, such as, for example, breaks in the forest canopy (especially in low *Nothofagus solandri* var. *cliffortioides*, *N. menziesii* and *Dracophyllum* forest), semi-open areas at the forest margin, and exposed rocky knolls. In the south it occurs in peat bogs of *Sphagnum*, *Oreobolus* and *Donatia* with species such as *Lepidothamnus laxifolius*. The species occurs on well-drained, often steep slopes and bryophyte-covered banks, usually on soil, particularly on infertile gleyed soils, in hummocks over very decayed stumps, on the tops of bryophyte-covered logs and rarely as an epiphyte (on *Weinmannia racemosa* trunk, a single record). It often is a component of bryophyte-rich (particularly hepatic-rich) sites. Associated species are *Adelanthus occlusus*, *Bazzania involuta*, *Blepharidophyllum vertebrale*, *Campylopus bicolor*, *C. clavatus*, *Chandonanthus squarrosus*, *Cryptochila grandiflora*, *C. pseudocclusa*, *Dicranoloma robustum*, *Gackstroemia weindorferi*, *Jamesoniella colorata*, *Lepidozia ulothrix*, *Racomitrium pruinosum* and *Wijkia extenuata*.

Comments: The shape and orientation of the leaves appears complex *in situ*, but is in fact fairly simple, once the leaves are removed from the stem. The leaves are moderately to strongly falcate and strongly channeled from base to apex, with broadly inflexed, entire margins (Fig. 147: 1). The dorsal half of the leaf lamina in attached leaves is vertically positioned (seen ± on edge in dorsal view), whereas the ventral half of the leaf appears strongly cupped. The leaves are virtually impossible to flatten under a coverslip, but if bisected longitudinally so they will lie flat, they are seen to be broadly elliptic to suborbicular in outline, with a broad, U-shaped sinus between the lobes. The dorsal lobe is usually distinctly smaller and narrower than the ventral. The surface of distal half of the leaf is rather obscurely striate-papillose but toward the leaf base becomes markedly long-striate and quite easily observed.

The species has two varieties.

Key to Varieties

1a. Leaf cell trigones bulging to nodulose, often confluent, the lumen stellate and surrounded mostly by the trigones; marginal cells of leaf with exposed wall distinctly thickened, the wall thickness equal to or exceeding the lumen diameter. Common . . . . . var. *schismoides* (p. 679)

1b. Leaf cell trigones straight-sided to somewhat bulging, never nodulose, normally not confluent, the lumen ± rounded at the corners, not stellate, surrounded mostly by the thin walls; marginal cells of leaf with exposed wall at most moderately thickened, the wall thickness considerably less than the lumen diameter. Rare and sporadic (in New Zealand) . . . . . var. *crassulum* (p. 680)

Anastrophyllum schismoides (Mont.) Steph. var. ***schismoides***

[Fig. 147: 1–6, 9–11; Fig. 148; Fig. 150: 1, 2, oil-bodies, p. 684]

Leaf cell trigones bulging to, more often, nodulose, often confluent, the cell lumen stellate and surrounded mostly by the trigones; marginal cells of leaf with exposed wall distinctly thickened, the wall thickness equal to or exceeding the lumen diameter.

This is the more common of the varieties.

Anastrophyllum schismoides var. ***crassulum*** J.J.Engel

[Fig. 147: 7, 8]

Anastrophyllum schismoides var. *crassulum* J.J.Engel *in* J.J.Engel & Braggins, J. Bryol. 20: 379. *f. 1: 7, 8.* 1998. Holotype: Tasmania, Gordon River, vicinity of Sir John Falls, just upriver from Butler Is., ca. 50 m, *Engel 14742 – c. per.* (F); isotype: (HO).

Leaf cell trigones straight- or even concave-sided to somewhat bulging, never nodulose, normally not confluent, the lumen ± rounded at the corners and surrounded mostly by the thin walls; marginal cells of leaf with exposed wall at most moderately thickened, the wall thickness considerably less than the lumen diameter.

The var. *crassulum* is rare and sporadic in New Zealand, but rather common in Tasmania. In New Zealand it occurs in Otago (455–610 m), Canterbury (875–950 m), Nelson (1035 m) and Auckland (Mt. Moehau, 800–860 m) provinces.

Anastrophyllum novazelandiae R.M.Schust.

Anastrophyllum novazelandiae R.M.Schust., Rev. Bryol. Lichénol. 34: 282. *f. 4.* 1966. Type: New Zealand, South Is., Fiordland Natl. Park, Route Burn track between Earland Falls and Lake Mackenzie, W slope of Humboldt Mtns., upper Hollyford Valley, ca. 4200–4500 ft., *Schuster 49471b.*

Plants wiry, erect to ascending, yellowish brown to chestnut, locally ± reddish, minute, to 15 mm high, 775 μm wide. Branching irregular or plants unbranched, pseudo-dichotomous, the plants seemingly furcate, the branching apparently exclusively terminal, *Frullania* type; half-leaf ovate-lanceolate, unlobed. Stems brownish, the cortical cells not or weakly differentiated, brownish, in 1–2(3) layers; medullary cells colorless, firm. Rhizoids very few, scattered. Leaves distant, subcontiguous above, pectinately distichous in orientation, stiffly and obliquely to widely spreading to subsquarrose, not dorsally secund or hardly so, the insertion oblique ventrally but transverse in dorsal 0.3; leaves narrowly to less often broadly ovate to elliptic-ovate, slightly to clearly longer than broad, strongly concave to loosely canaliculate-folded, 220–300 μm wide × 280–330 μm long, bifid to 0.35–0.4; lobes inflexed, acute, subequal to distinctly unequal (the dorsal half of leaf 0.35–0.45 the area of ventral), terminating in a single cell or a uniseriate row of 2 cells, the sinus acute; lamina and lobe margins at least in part crenulate by the bluntly projecting anticlinal walls of the marginal cells but otherwise entire; dorsal margin not decurrent, sometimes with a stalked slime papilla or tooth at base. Cells of leaf small, firm, with sinuous walls, with distinct, bulging trigones and irregular intermediate thickenings, the median leaf cells (10)12–14 μm wide × 16–22(24) μm long; basal cells elongated, commonly ca. 2:1, often in longitudinal rows; surface smooth. Oil-bodies (Schuster, 1966c) (3)4–9(10) per median and basal cell, 0–1 oil-bodies per marginal lobe cell, 4–8 per intramarginal lobe cell, rather glistening, appearing almost homogeneous (the spherules non-protuberant), spherical to ovoid, very small, 1.2–1.5 × 1.5–2 μm to 2.2 × 3–3.5 μm. Underleaves absent, or present as a uniseriate filament of up to 7(10) cells, less often biseriate (at least in basal portion), terminating in a slime papilla, the ventral merophyte 1 or at most 2 cells wide. Asexual reproduction lacking. Otherwise unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (ca. 1010–1615 m). Known from Fiordland, Otago, Westland and Marlborough EPs. Known from only five collec-

tions: from the type, from Mt. Alexander near Caswell Sound, Mt. Shrimpton near Makarora, Branch River and Mt. Richmond, both in Marlborough. On Mt. Richmond it was found with *Acrolophozia pectinata*, *Chandonanthus squarrosus*, *Cladia aggregata*, and *Racomitrium crispulum* on a dripping rock face at ca. 1615 m. The type material was admixed with *Cuspidatula monodon*, *Metzgeria* sp., *Pseudomarsupidium piliferum*, *Frullania* sp. and *Cephaloziella* sp., growing on an exposed, moist crag in the snow tussock zone just above tree line. At the Branch River site, it was found on a greywacke boulder in *Festuca novae-zelandiae* tussockland on the valley floor, with *Andreaea mutabilis*, *Polytrichum juniperinum*, *Menegazzia pertransita* and *Rhizocarpon geographicum*. At the Mt. Shrimpton site it occurred on soil on a rock outcrop with *Cheilolejeunea albovirens*, *Ditrichum punctulatum*, *Gymnomitrion cuspidatum* and *Notoligotrichum australe*. On Mt. Alexander, it was among *Plagiochila circinalis* but no other habitat information was recorded.

Comments: This poorly known species is sharply distinct from *Anastrophyllum schismoides* by the minute size of the plants, the presence of terminal, *Frullania*-type branching, and the widely spreading, ± symmetrically bilobed leaves that are not dorsally falcate-secund, the margins (at least in part) distinctly crenulate by the swollen, projecting radial walls of the marginal cells.

Anastrophyllum papillosum J.J.Engel & Braggins

[Fig. 149]

Anastrophyllum papillosum J.J.Engel & Braggins, J. Bryol. 20: 381. *f. 3*. 1998. Holotype: New Zealand, North Is., Wellington Prov., Tongariro Natl. Park, Soda Springs, Mangatepopo Stream, NE of Whakapapa Village, 1350 m, *Braggins 97/106B* (F); isotypes: (AK, CHR 558817).

Plants stiff, wiry, erect, deep reddish pigmented, minute, to 10 mm high, 800 μm wide. Branching sparse, the branches nearly exclusively lateral-intercalary, from ventral end of leaf axil; *Frullania*-type branches rare. Stems castaneous, the cortical cells not or weakly differentiated, brownish, in 1–2 layers of very thick-walled cells; medullary cells brownish, firm, the inner core of cells somewhat larger. Rhizoids few, in isolated patches in median and basal sectors of stem, nowhere dense, scattered. Leaves rigid and firmly attached, approximate to loosely imbricate (distant to contiguous on weaker shoots), stiffly obliquely to widely spreading to ± squarrose, weakly dorsally assurgent, the insertion oblique in ventral half, transverse in dorsal half; leaves narrowly ovate to elliptic-ovate, slightly to clearly longer than broad, strongly concave to loosely canaliculate-folded, 200–220 μm wide × 270–280 μm long, bifid to (0.35)0.4–0.45; lobes inflexed, acute, subequal or the dorsal often somewhat smaller (often a bit narrower than but only occasionally shorter than the ventral), the summit bluntly rounded (then without a uniseriate row of cells) or angled (the uniseriate row then terminating in a single cell or, occasionally, a uniseriate row of 2 cells, the tip then subapiculate), the sinus acute; leaf margins often with the outer row of cells bleached out, the margins of lobe and distal half of lamina crenulate by the dilated, bluntly projecting, anticlinal walls of the marginal cells, the margins in basal half of lamina smooth or with only feebly projecting septa; dorsal margin not decurrent, at times with a stalked slime papilla or blunt tooth at base. Cells of leaf markedly thick-walled, with bulging trigones, intermediate thickenings absent, the median leaf cells 13–21 μm wide and long; basal cells typically not or at most moderately elongated (1–1.7:1), rarely ca. 2.5:1, in ± longitudinal rows; surface closely papillose on lobes, the

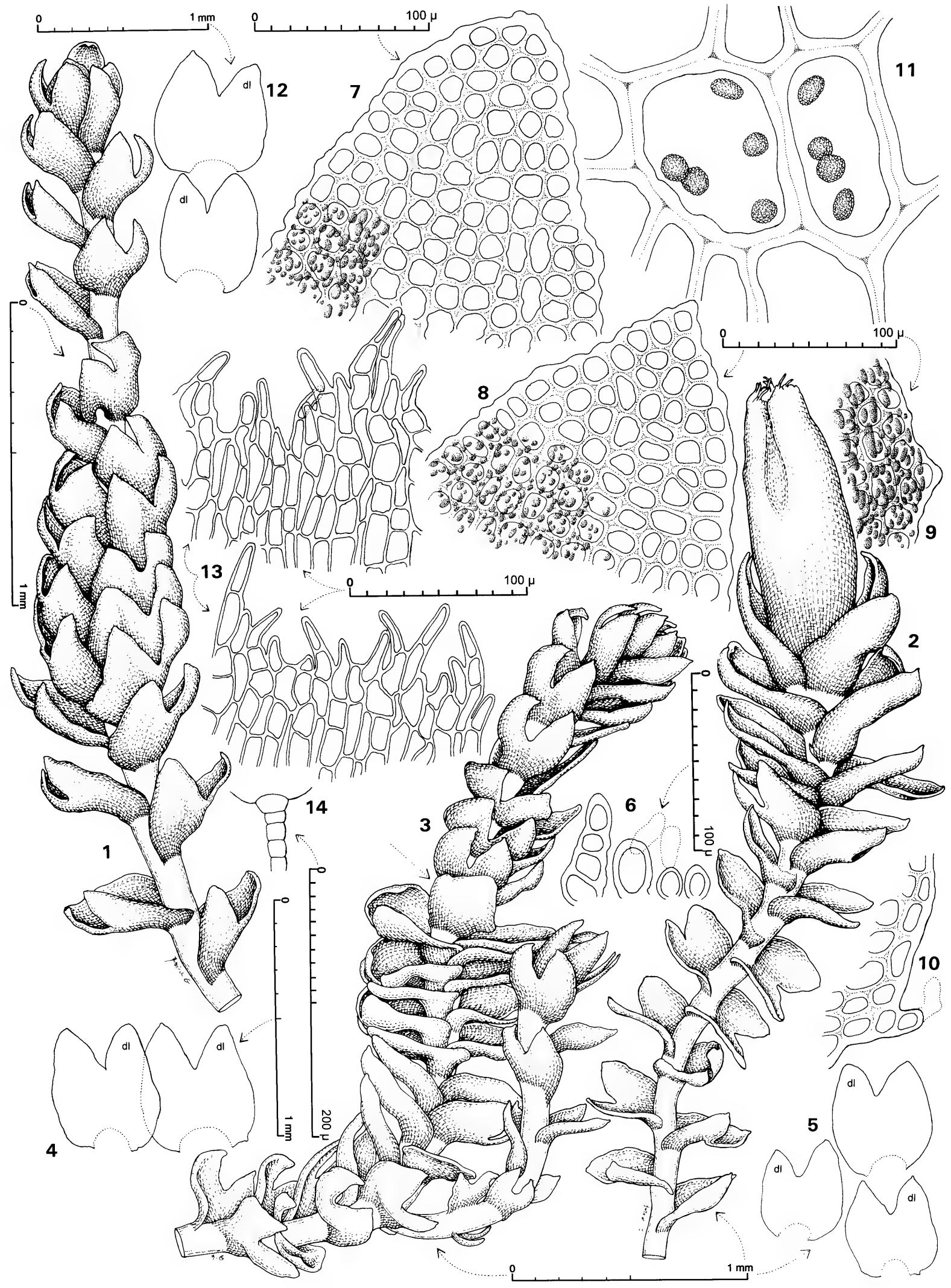

Fig. 149.
Anastrophyllum papillosum J.J.Engel & Braggins. 1. Leading shoot with intercalary androecium, dorsal view. 2. Leading shoot with gynoecium, dorsal view (note dorsal sectors of 2 subfloral leaves not shown to reveal insertions). 3. Main shoot with lateral-intercalary branch (note the branch originates from ventral end of leaf axil; note also the undivided leaf, at arrow), dorsal-lateral

lamina closely striate-papillose. Oil-bodies (2)3–5(6) per median and marginal cells of lobe, the basal cells of lamina (2)3–6(7) per cell, ± glistening, opaque, finely granular, the spherules minute and non-protuberant, the oil-bodies spherical and 2.9 μm in diam. to elliptic and 2.9 × 3.9–4.9 μm, sporadically linear and 2 × 4.9 μm. Underleaves present (but apparently disappearing in older shoot sectors), consisting of a single cell or a uniseriate filament of up to 4 moderately to very thick-walled cells, often terminating in a slime papilla, the ventral merophyte 1 cell wide. Asexual reproduction lacking.

Dioecious. Androecia on main shoots terminal, but becoming intercalary with age, with up to 4 ♂ sectors per shoot, the androecia about as wide as vegetative sectors, with up to 5 pairs of bracts; bracts ventricose-cucullate, 2-lobed to ca. 0.35, the lobes broad acute, the tips angular to (often) bluntly rounded, the dorsal margin of lamina not dilated, entire; antheridia 1 per bract, the stalk short, uniseriate; paraphyllia not seen. Gynoecia on main shoots, without subfloral innovations; innermost bracts much larger than both leaves and bracts below, straight, not falcate, approximate to loosely imbricate, deeply concave, ± symmetrically bifid to ca. 0.35(0.5), the lobe tips bluntly rounded, occasionally angular, sporadically apiculate; lamina margins entire; bracteole lacking. Perianth narrowly elliptic to oblong, tapering to the mouth, rather shallowly plicate in distal ca. 0.25–0.35; mouth bleached, crenate-subciliate by feebly to wholly projecting, evenly thick-walled cells, the longest mouth ornamentation consisting of a uniseriate row of 3 moderately elongated cells; cells immediately below mouth (bleached sector) typically short-rectangular to occasionally elongate, exceptionally somewhat irregular in shape, the walls evenly thickened, the cells of the perianth proper similar to those of the leaves.

Seta elevating capsule well above perianth, the seta seen only in collapsed state. Capsule irregularly dehiscing into 5 valves, the longest only 415 μm long, the walls semi-collapsed (the cross section data not available); outermost layer of cells with radial walls with red-brown, rather close, nodule-like to short and blunt spine-like thickenings; innermost layer of cells irregularly long-rectangular, the walls with semiannular bands common, for the most part complete, rarely forked.

Spores and elaters not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (870 m), North Island (1350 m).

In the South Island known only from a mosaic of scrub and grassy areas near the Temple Basin ski area (Arthur's Pass Natl. Park) and on a rock wall near a waterfalls in the upper reaches of a *Podocarpus* forest just below Wakefield Falls (east-facing slope of Mt. Wakefield, Mt. Cook Natl. Park, 870 m). The type locality (North Island) is an area in the alpine zone with low fellfield vegetation. At this station plants occurred in a humus mat over rock of steeply sloping, south-facing, irregular cliffs associated with waterfalls, and grew vertically, with the stem tips emergent from the dense mat of *Temnoma quadripartitum*; also present are occasional stems of *Triandrophyllum subtrifidum*, *Lepidozia laevifolia* and *Pachyschistochila* sp. Small fronds of the fern *Hymenophyllum multifidum* are present.

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view. 4, 5. Leaves (dl = dorsal lobe). 6. Four underleaves. 7. Distal sector of dorsal lobe (surface detail shown in part). 8. Distal sector of ventral lobe (surface detail shown in part). 9, 10. Base of dorsal margin of leaf showing small tooth (both figs. drawn to same scale). 11. Leaf cells with oil-bodies (× 1270). 12. Innermost ♀ bracts from same gynoecium (dl = dorsal lobe). 13. Portions of perianth mouth. 14. Antheridial stalk. (All from holotype.)

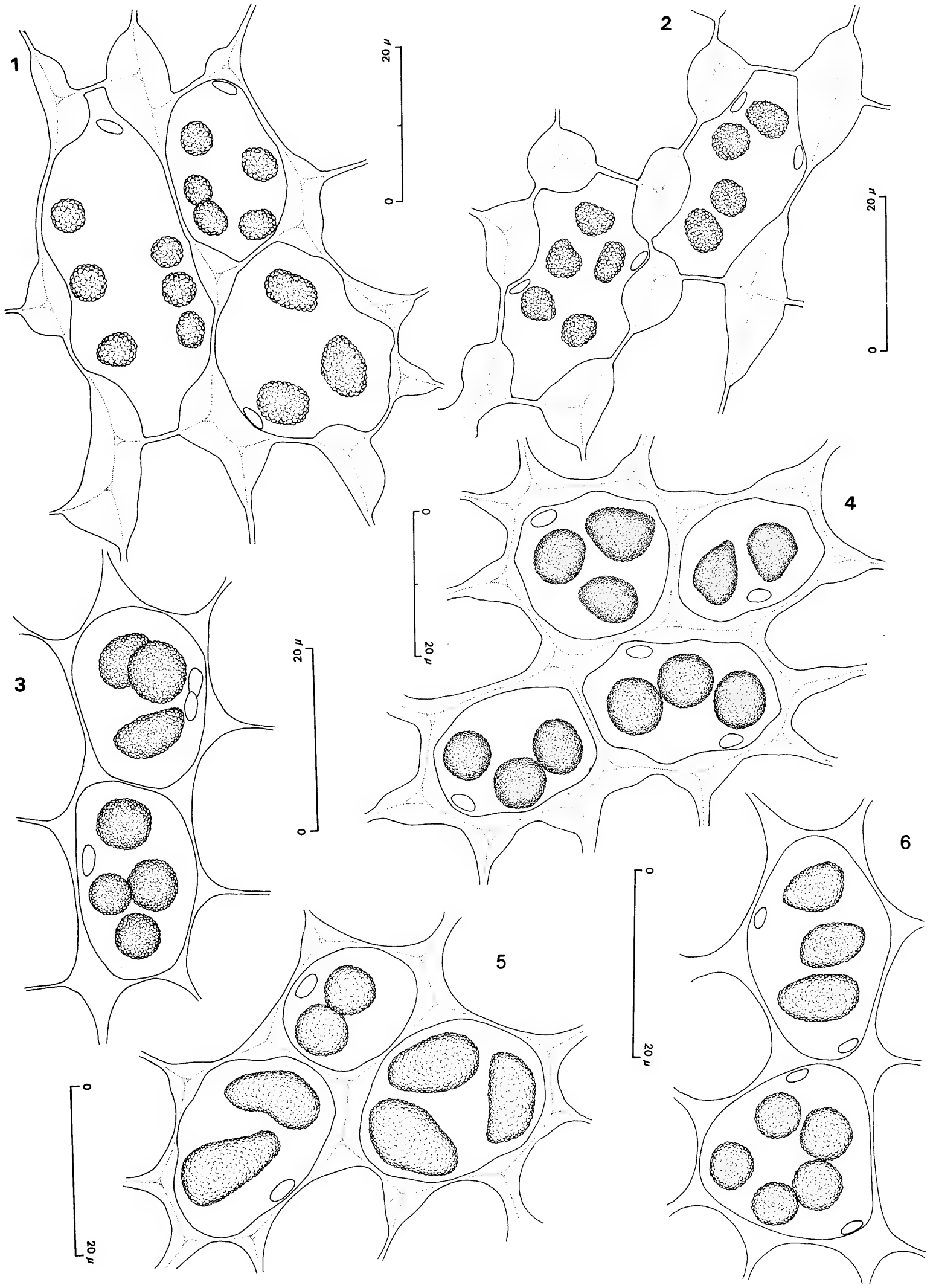

Fig. 150.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Anastrophyllum schismoides* (Mont.) Steph. Basal cells of lamina. 2. *Anastrophyllum schismoides* (Mont.) Steph. Cells of lobe base. 3. *Andrewsianthus cuspidatus* R.M.Schust. Cells at lobe base. 4. *Andrewsianthus perigonialis* (Hook.f. & Taylor) R.M.Schust. Median lamina cells. 5. *Andrewsianthus cuspidatus* R.M.Schust.

Comments: The species is related to *Anastrophyllum novazelandiae*, but differs from that species by the sparse branching, which is only lateral-intercalary (Fig. 149: 3); the strongly striate-papillose surface (Fig. 149: 7–9) vs. smooth in *A. novazelandiae*; and the not or hardly elongated basal lamina cells, which are usually 1–1.7:1 and only rarely ca. 2:1. Moreover, the projecting septa of the marginal cells are only feebly or not at all present in the basal half of the leaf lamina, whereas in *A. novazelandiae*, these protruding walls are present throughout the leaf margin (Schuster, 1966c, fig. 4: 9). Oil-bodies are small and glistening as in *A. novazelandiae*, but differ in being finely granular (Fig. 149: 11) and with a similar number in all lobe cells. In *A. novazelandiae* the oil-bodies are nearly homogeneous, only 0–1 per marginal cell, but with 4–8 in intramarginal lobe cells.

Confusion may arise from differentiating this species from populations of *Andrewsianthus cuspidatus* that only occasionally become flagelliform at the shoot tips; for comments see under that species.

Andrewsianthus R.M.Schust.

Andrewsianthus R.M.Schust., Rev. Bryol. Lichénol. 30: 66. 1961.
Cephalolobus R.M.Schust., Rev. Bryol. Lichénol. 34: 244. 1966.

Plants usually loosely procumbent, golden brown to red-brown, the leafy shoots typically becoming attenuate and flagelliform, the flagella either plagiotropic and remaining on the substrate surface (subg. *Cephalolobus*) or abruptly geotropic and penetrating the substrate (subg. *Andrewsianthus*); other geotropic flagelliform axes arising from normal-leaved shoot sectors usually lacking, and the leafy shoots not arising from a system of creeping stoloniform axes. Branches lateral-intercalary, arising from near the juncture of the leafy shoot sectors and attenuated flagella, originating either from the leaf axil, thus lateral in position (subg. *Cephalolobus*) or from dorsal end of leaf axil, and arching up and away from the parent stem (subg. *Andrewsianthus*); ventral-intercalary branches present in a few species (e.g., *A. planifolius*); *Frullania*-type branches absent (except in *A. achrous* and subg. *Pseudotritomaria*). Stems rigid, wiry, narrow for shoot size, the cortex usually well developed, in 1–2 layers of thick-walled cells, the cortex and medulla without mycorrhizal infection. Rhizoids few or lacking on normal-leaved shoot sectors, but sporadic to frequent on flagelliform sectors. Leaves with insertion subtransverse to succubous, the insertion extending to but not beyond the dorsal stem midline, the leaves usually bilobed, unlobed in a few species, trilobed in subg. *Pseudotritomaria* but very rarely elsewhere, the lobes entire, the lamina margins entire or with a few slime papillae near dorsal base. Cells with trigones distinct, at times moderately nodose, the cells of moderate size (ca. 20–30 μm in diam. at leaf middle); surface striolate-papillose. Oil-bodies usually 2–5 per cell, finely granular, medium to rather large. Underleaves lacking or

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Median lamina cells. 6. *Andrewsianthus perigonialis* (Hook.f. & Taylor) R.M.Schust. Cells of upper leaf middle. (Figs. 1, 2, from *Glenny 9192*, New Zealand, South Is., Westland EP, Okarito, Kohuamarua Bluff track; 3, from *Glenny 9206*, New Zealand, South Is., Westland EP, Upper Otira Valley; 4, from *Engel 27283*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Otira Valley Track; 5, from *Glenny 9335*, New Zealand, Stewart Is., Gog; 6, from *Glenny 9321*, New Zealand, Stewart Is., Belltopper Falls.)

vestigial (ventral merophytes narrow), lanceolate or (often) consisting of 1–3 stalked slime papillae. Asexual reproduction lacking (except with gemmae only in *A. kilimanjaricus*).

Dioecious. Androecia terminal but becoming intercalary on leading leafy axes, laxly spicate, the bracts spreading, with 1(2) sharp teeth at dorsal base; antheridia 1(2) per bract, the stalk uniseriate. Gynoecia terminal on leading leafy axes, the bracts in 1–3 gradually larger series, those of innermost series usually bifid, the lobe and lamina margins variously dentate to laciniate, less often entire; bracteole distinct, at times strongly connate on 1 side, usually (at times asymmetrically) bilobed (undivided in *Andrewsianthus australis*), armed like bracts or entire. Perianth terete below, pluriplicate distally, contracted to the mouth, the mouth lobulate, the lobules ciliate-laciniate to ciliate, with a uniseriate row of up to 7 cells.

Seta massive and of many cells or of 12+4 type. Capsule ellipsoidal, the wall 3(4)-stratose; outer layer of cells with strong nodular thickenings; inner layer of cells with semiannular bands, the bands mostly complete, at times branching and anastomosing to form local fenestrae.

Spores baculate, the bacula cylindrical, somewhat longer than wide and truncate at the apex (*Andrewsianthus australis*) or minutely spinulose. Elaters 2(3)-spiral, the spore:elater diam. ratio ca. 4:1.

Type: *Andrewsianthus puniceus* (Nees) R.M.Schust. *ex* Grolle (≡ *Jungermannia punicea* Nees)

A genus of ca. 25 species found chiefly in the Asian tropics and the southern temperate regions. Schuster (2002a) recognized three subgenera:

1) subg. *Cephalolobus* (R.M.Schust.) R.M.Schust. is strictly south temperate; *Andrewsianthus sphenoloboides* (R.M.Schust.) R.M.Schust. *ex* J.J.Engel and *A. scabrellus* (C.Massal.) R.M.Schust. *ex* J.J.Engel (Engel, 2007) occur in southern South America and two species occur in New Zealand.
2) subg. *Andrewsianthus* has several Austral species. *Andrewsianthus australis* J.J.Engel occurs in southern Chile and the Falkland Islands (Engel, 1972, 1978, 1990a) and *A. planifolius* J.J.Engel is endemic to the Falkland Islands (Engel, 1972, 1990a). *Andrewsianthus bilobus* (Mitt.) Grolle is widespread in Africa, including South Africa (cf. Grolle, 1963c; Wigginton & Grolle, 1996; Schuster, 2002a). Two species are endemic to Marion Island, *A. carinatus* Grolle and *A. marionensis* (S.W.Arnell) Grolle. *Andrewsianthus lancistipulus* Grolle of Marion Island was placed in *Lophozia* by Schuster (2002a, p. 259). One species, *A. perigonialis* (Hook.f. & Taylor) R.M.Schust., occurs in New Zealand.
3) subg. *Pseudotritomaria* R.M.Schust., Beih. Nova Hedwigia 119: 323. 2002, has only *A. ferrugineus* Grolle (Grolle, 1966f), known only from high elevations (4000 m) in Nepal and Bhutan.

Species of *Andrewsianthus* at times may be confused with *Anastrophyllum novazelandiae* and *A. papillosum* as well as small plants of *Lophozia autoica* or *L. multicuspidata* (all subfam. *Lophozioideae*) or even species belonging to other families, such as *Acrolophozia*, *Marsupella* and others. These taxa are all of a similar, rather small size with bifid, transversely oriented leaves, have underleaves that are reduced or lacking and have reddish and/or golden brown secondary pigments; a number of these "look-alikes" also have coarse trigones and a strongly papillose surface. The following key to *Andrewsianthus* and similar genera emphasizes characters found in sterile plants.

Key to *Andrewsianthus* and similar-appearing genera

1a. Leafy shoots regularly becoming attenuate, flagelliform, microphyllous and rhizoid-bearing distally, the attenuated shoot apex often abruptly arcuate or geotropic; leaves conspicuously decreasing in size distally; branching (in ours) all intercalary, some or many usually dorsal, of *Andrewsianthus* type; gemmae lacking (in ours). Leaf insertion subtransverse to succubous . . . . . *Andrewsianthus*

1b. Leafy shoots not becoming flagelliform and microphyllous distally, the shoot apex not abruptly arcuate or geotropic; leaves not conspicuously decreasing in size distally; branching various, at times terminal, but never with dorsal-intercalary, *Andrewsianthus*-type branches; gemmae at times present 2

2a. Leaf lobes frequently abaxially ± concave to sulcate 3

3a. Plants yellow-brown to fulvous; branching all lateral-intercalary; perianth not or barely emergent beyond ♀ bracts, the perianth + bracts forming a capitulum . . . . . *Acrolophozia* [*Gymnomitriaceae*] (p. 785)

3b. Plants purplish to piceous; branching normally all ventral-intercalary; perianth long-emergent beyond ♀ bracts, the perianth + bracts not forming a capitulum . . . . . *Allisoniella* [*Cephaloziellaceae*] (p. 570)

2b. Leaf lobes plane or adaxially concave 4

4a. Leaf insertion (in ours) interlocking dorsally; gynoecia forming a ring- or tube-like fleshy stem perigynium, the ♀ bracts erect, arising from the perigynium, the perianth short, included within the uppermost bracts. Plants reddish brown or piceous to black; cells with coarse trigones, the surface smooth; leaf insertion transverse, at least in dorsal half; branching all lateral-intercalary . . . . . *Marsupella* (p. 798)

4b. Leaf insertion extending to but not beyond stem midline dorsally, in some taxa the insertion not extending to stem midline and then defining a leaf-free strip; gynoecia not forming a stem perigynium, the perianth conspicuous, clearly emergent beyond uppermost bracts 5

5a. Cells leptodermous, trigones lacking. Stem cortical cells larger than the medullary . . . . . *Metahygrobiella* + *Cephalozia* [*Cephaloziaceae*] (p. 551)

5b. Cells (in ours) with at least small trigones, many taxa with trigones conspicuous, large and bulging 6

6a. Leaves with dorsal third or more of insertion transverse, except at times for a decurrent strip along the dorsal stem midline, the orientation transverse; plants erect or suberect; rhizoids sparsely developed, (in ours) if present nowhere dense and not developed near shoot apex . . . . . *Anastrophyllum* (p. 673)

6b. Leaves with at least the dorsal half of insertion clearly succubous, the dorsal end directed toward the shoot base, the orientation oblique to horizontal; plants typically loosely creeping to ascending; rhizoids often present and dense throughout, including near shoot apex . . . . . *Lophozia* (p. 645)

Andrewsianthus and *Anastrophyllum* are very similar in appearance and further studies of this complex should center around the delimitation of these genera. For example, species of *Andrewsianthus* subg. *Cephalolobus* have transversely oriented leaves with the dorsal sector of the insertion transverse, just as in *Anastrophyllum*. Moreover, the taxa of subg. *Cephalo-*

lobus also tend to form lateral-intercalary branches from the median sector of the leaf axil, i.e., dorsal-intercalary, *Andrewsianthus*-type branches are not developed. The branch position is very similar to the position that is so very often found in *Anastrophyllum*. Schuster (2002a, p. 321) remarked that taxa in subg. *Cephalolobus* "suggest that *Andrewsianthus* evolved from *Anastrophyllum*-like ancestral types…and that ultimately it is the universal proclivity for shoot apices to become, usually rather abruptly microphyllous, rhizoid-bearing, and—mostly—geotropic, which is most crucial in delimiting the genus..." One of the difficulties inherent in work with this complex is that some populations of *Andrewsianthus* only sporadically produce microphyllous flagelliform shoot tips, and these may easily be overlooked. Therefore, a careful search is required to assess the degree of expression of this character.

Species descriptions were adapted, but freely modified, from Schuster (1966c); the generic description and key is adapted but considerably modified from Schuster (2002a).

References: Engel (1972); Grolle (1962b, 1971a); Schuster (1966c, 1968b, 2002a); Váňa (1985).

Key to Species

1a. Leaves bifid to 0.2–0.4(0.55), the lobes acute to cuspidate; leaf surface markedly coarsely papillose, the papillae often hemispherical, the surface becoming striate-papillose toward leaf base; underleaves consistently present; ♀ bract lobes ± acute, often ± toothed 2

2a. Underleaves vestigial to small (rarely to 0.25× leaf area); stem and leaf bases smooth, without cellular processes; ♀ bract lobes ± weakly toothed or entire . . . . . *A. cuspidatus* (p. 688)

2b. Underleaves 0.5× leaf area; stem and leaf bases ± armed with cellular processes; ♀ bract lobes ± coarsely spinose-dentate . . . . . *A. hodgsoniae* (p. 691)

1b. Leaves bifid to 0.15–0.2, the lobes blunt to at times obtusely rounded; leaf surface weakly striate-papillose or if roughened, then striate, even in basal sector of lobes; underleaves lacking or comprised of a cluster of a few cells; ♀ bract lobes blunt, entire-margined . . . . . *A. perigonialis* (p. 692)

Subg. ***Cephalolobus*** (R.M.Schust.) R.M.Schust.

Subg. *Cephalolobus* (R.M.Schust.) R.M.Schust., Beih. Nova Hedwigia 119: 326. 2002. Type: *Cephalolobus scabrellus* (C.Massal.) R.M.Schust.

Andrewsianthus cuspidatus R.M.Schust.

[Fig. 150: 3, 5, oil-bodies, p. 684]

Andrewsianthus cuspidatus R.M.Schust., Beih. Nova Hedwigia 119: 331. 2002, *nom. nov. pro Cephalolobus squarrosus* R.M.Schust., Rev. Bryol. Lichénol. 34: 256. *f. 2*. 1966, *non Andrewsianthus squarrosus* (S.W.Arnell) Grolle ≡ *Lophozia squarrosa* S.W.Arnell, Results Norweg. Sci. Exped. Tristan da Cunha 42: 20. 1958 (Tristan da Cunha). Type: New Zealand, South Is., Mt. Cook Natl. Park, Sealy Ra., below Sealy Lakes, ca. 4000 ft., *Schuster 49713*.

Plants firm, green to greenish brown to yellow-brown, the stems often darker, at times red-brown, the attenuated flagella often similarly, intensely pigmented (but reddish pigments not seen in leaves), the plants occasionally to commonly becoming flagelliform at shoot tips, the shoots to 685(715) μm wide. Branching rather sparing, the branches all lateral-intercalary, axillary in position and not from dorsal end of leaf axil, arising from a ± brownish, creeping, microphyllous rhizome; branches occasionally becoming flagelliform and rhizoidous distally, then in turn giving rise to normal, flexuous, leafy stems. Stems slender for plant size, with cortical cells in surface view often almost guttulate to rounded-oblong, ventrally and latero-ventrally becoming narrower and often longer, the surface rather coarsely striolate but without cellular excrescences, the cortex in cross section in a single layer of very thick-walled cells; medullary cells becoming larger toward middle of stem, hyaline. Rhizoids scattered, few, usually colorless. Leaves rigid, brittle, remote to subcontiguous, widely spreading to squarrose, the base erect and somewhat sheathing, the dorsal sector of leaf antically assurgent and seen edge on or suberect and then the leaf weakly folded (but ecarinate), the leaf lobes widely spreading to squarrose, subtransversely inserted and transversely oriented but somewhat dorsally arched or assurgent, the leaves oblong to oblong-obovate, clearly longer than wide, on sterile stems 2–3× stem width, 265–315 μm wide × 330–415 μm long, bifid (rarely trifid) to 0.2–0.4(0.5); lobes acute, usually narrowly and often sharply so, at times subapiculate to cuspidate, terminating in a single cell or a uniseriate row of 2 (very rarely 3) cells, the tip cell of the lobes wider than long, subisodiametric or to 1.7× longer than wide, the lobe tips often appearing hyaline and scorched; sinus V-shaped but often with base of V narrowly rounded; margins of lobe and lamina crenulate by the dilated, bluntly projecting, anticlinal walls of the marginal cells (even at leaf base), the margins otherwise entire, very rarely with a tooth near dorsal base. Cells with trigones strong, large and bulging, the cells of lobe margins 13–16 μm wide, the median lamina cells rather small, 13–19 μm wide × 17–25(27) μm long, those of leaf base not or hardly larger; surface with coarse, often hemispherical papillae (the largest 5–5.5 × 7–9 μm), becoming striate-papillose toward the base. Oil-bodies (Schuster, 1966c, 2002a) occupying conspicuous portion of cell lumen, 2–4 per cell, rather glistening, faintly granulate at best, very large, variable in form, spherical and 5.5–6.5 μm in diam. to ovoid or ellipsoidal and from 5.5–7 × 6–8 μm to 6–7.5 × 10–13 μm. Oil-bodies (*Glenny 9206*, *9335*) similar throughout leaf, occupying a large portion of the cell lumen, pale smokey grey, the lobes and disc with 2–3 or (2)3–4(5) per cell, even toward lobe tips and at the leaf base, finely to coarsely granular, spherical to broadly ellipsoidal, often somewhat irregularly so, the larger ones often with 1–2 depressions, the oil-bodies 4.5–7 × 6–13 μm, some massive, especially in cells with 2 oil-bodies per cell. Chloroplasts much smaller than oil-bodies. Underleaves consistently present, usually very small (rarely to 0.25× leaf area) and often consisting of a basal tier of 2–4, very thick-walled cells hardly longer than wide, capped with 2 slime papillae, or the thick-walled basal cells with 2 somewhat elongated, thin-walled cells each with a slime papilla, less commonly with a uniseriate row of several cells, the underleaves exceptionally bifid or lamelliform and then to 5 cells wide at base, undivided and with a few marginal small teeth; ventral merophytes relatively narrow, 1–2 cells broad. Asexual reproduction lacking.

Androecia terminal but becoming intercalary on leading leafy axes, laxly spicate, the bracts concave-ventricose throughout; antheridia 1 per bract, the stalk uniseriate. Gynoecia with bracts in 3 series, those of innermost series 2(3)-lobed, at times asymmetrically so, the lobe margins entire or with a tooth or at times with several coarse teeth; bracteole conspicuous, 0.5–0.75× bract area, free from bracts, asymmetrically bilobed, the lobe and lamina margins entire or with a tooth or at times with several coarse teeth. Perianth terete below, bluntly trigonous-

triplicate in distal ca. 0.5, contracted to the lobulate mouth, the lobules spinose-dentate to subciliate, with a uniseriate row of up to 3 cells.

Sporophyte not seen.

Distribution and Ecology: New Zealand: Stewart Island (600–690 m), South Island (695–1740 m), North Island (1080–1450 m); Australia: Tasmania. In New Zealand known from Fiordland, Otago (Remarkables, Ocean Peak), Westland (Taipo Valley, Otira Valley), Canterbury (Mt. Cook Natl. Park, upper Godley River, Harman Pass, Torlesse Ra.), Western Nelson (Paparoa Ra., Cobb Valley) and Volcanic Plateau (Mt. Ruapehu) EPs.

This species typically is associated with rock. It occurs over boulder faces, usually where soil or silt has accumulated, particularly in niches such as crevices or pockets, deep in recesses between rocks or under rock overhangs. The boulders or outcrops often occur in rather exposed situations. On Stewart Island it occurs in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* from 0.5–2 m tall and significant areas of exposed rock (Mt. Rakeahua summit area, 600–690 m). In Canterbury it is found in late snowbank sites at the upper limit of continuous vegetation among *Marsippospermum gracile* and *Poa colensoi* rushland or with small *Celmisia* species. At the south end of Lake Marion (Fiordland Natl. Park, 695 m) it occurred with *Herbertus oldfieldianus* on the face of a shaded, wet huge boulder near the lake, at the edge of a rather open forest dominated by *Nothofagus menziesii*. Also found on a rock face in the vicinity of a waterfalls in the upper reaches of a *Podocarpus* forest (just below Wakefield Falls, Mt. Cook Natl. Park, 870 m). In the Gertrude Valley occurring in a mat of bryophytes on a boulder face in a mosaic of large boulders and dense penalpine scrub (near track entrance to Gertrude Valley, Fiordland Natl. Park, 740 m). In the North Island occurring at Taranaki Falls Track (Tongariro Natl. Park, 1080 m) on the face of a huge boulder at the margin of a creek in a steep-sided canyon through a forest of *Nothofagus solandri* var. *cliffortioides*, *Griselinia littoralis*, *Pseudopanax colensoi* and *Podocarpus hallii*. Also in the alpine zone at 1450 m (Blyth Hut to Whakapapa Track not far from Bruce Road to Whakapapa Skifield, Tongariro Natl. Park).

The type is from ca. 1220 m in the Sealy Ra. (Mt. Cook Natl. Park), over damp, shaded rocks along an intermittent watercourse, admixed with *Gymnomitrion cuspidatum*, *Acrolophozia pectinata*, *Triandrophyllum* sp., *Jamesoniella* sp., *Diplophyllum* sp., *Andreaea* sp. and *Hymenophyllum multifidum*. In alpine sites it is commonly found in with *Andreaea acuminata*, *Bartramia papillata*, *Cryptochila grandiflora*, *Herzogobryum teres*, *Jamesoniella colorata*, *Radula sainsburiana* and *Rhacocarpus purpurascens*.

Comments: This species is closely allied to *Andrewsianthus hodgsoniae*. However, the leaf cells in *A. cuspidatus* are less coarsely papillose than those of *A. hodgsoniae*, and the stem is nearly smooth, having relatively low, welt-like striae vs. the coarse, hyaline papillae and scattered, conical to finger-like cellular outgrowths of the stem in *A. hodgsoniae*. The leaves of *A. cuspidatus* tend to be larger, always clearly longer than broad, and have the very sharp lobes that are commonly distinctly squarrose, giving the plant a different aspect from that of *A. hodgsoniae*.

Leaf lobe shape is variable, and part of the plasticity is due to the caducous cells at the lobe tip. The lobes terminate in a single cell or a uniseriate row of 2 cells. The tip cell of the lobe is variable, being wider than long, subisodiametric or up to 1.7× longer than wide, and is rounded at the tip or (often) tapers to a rather sharp summit that is thick-walled and ± protracted. In lobes that have a uniseriate row of 2 cells the penultimate cell is often wider than long. The tip cell or both cells of the uniseriate row, when present, often become hyaline,

scorched and ultimately collapse. The lobe tip then terminates in a pair of laterally juxtaposed cells and then is of a different shape, i.e., more narrowly rounded. Leaf lobes near the shoot apex are usually less eroded and should be checked for shape.

Andrewsianthus cuspidatus should not be confused with *Anastrophyllum papillosum*, particularly in those populations of *A. cuspidatus* that only occasionally become flagelliform at the shoot tips. At least some arching and geotropic flagelliform shoot tips may be found after a careful search; these are never present in *Anastrophyllum papillosum*. Also, *A. cuspidatus* has uniformly intercalary branches, the leaf margins are nearly always entire, and only golden brown pigments are developed, at least in the leaves. *Anastrophyllum papillosum* may produce *Frullania*-type branches, though rare, but the leaves commonly have a small tooth at the dorsal base and plants develop deep reddish pigmentation.

The species appears to be a close ally of *Andrewsianthus marionensis* (S.W.Arnell) Grolle (type: Marion Island) = *Andrewsianthus squarrosus* (S.W.Arnell) Grolle ≡ *Lophozia squarrosa* S.W.Arnell (type: Tristan da Cunha) (see Grolle, 1971a and Váňa, 1985). Schuster (2002a, p. 331) stated that *Lophozia squarrosa* S.W.Arnell of Tristan da Cunha "appears to be very closely allied, if not identical, with…*A. cuspidatus* R.M.Schust." Schuster (2002a, p. 327, key) mentions "New Zealand, Tristan?" in reference to *A. cuspidatus* R.M.Schust., indicating some doubt. We would prefer to recognize two distinct species—*Andrewsianthus marionensis* from Marion Island and Tristan da Cunha, and *A. cuspidatus* from New Zealand.

Andrewsianthus hodgsoniae (R.M.Schust.) R.M.Schust. *ex* J.J.Engel

Cephalolobus hodgsoniae R.M.Schust., Rev. Bryol. Lichénol. 34: 254. *f. 1*. 1966 ("*hodgsonae*").
Andrewsianthus hodgsoniae (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, Novon 17: 311. 2007. Holotype: New Zealand, South Is., Mt. Cook Natl. Park, Sealy Ra., above Sealy Lakes, ca. 4500–4900 ft., *R. & O. Schuster 49702*.

Plants *Cephaloziella*-like in appearance, wiry, rather rigid, ascending to suberect, dull green, at least locally (e.g., in leaf lobes) brownish to reddish brown, small to minute, to 480 μm wide. Branching common, the branches uniformly lateral-intercalary, from near middle of leaf axil, occasionally becoming flagelliform and rhizoidous. Stems large for plant size, in surface view covered with close, coarse, hyaline papillae and scattered, conical to finger-like cellular outgrowths, the stem surface dull, rough and irregular, in cross section with the cortical cells thick-walled, greenish brown or ± brownish, not sharply differentiated, a little smaller than the medullary cells; medullary cells with the inner cells hyaline and distinctly larger than the peripheral ones, quite collenchymatous. Rhizoids few to frequent, colorless, scattered. Leaves erect or suberect to obliquely spreading, not dorsally assurgent, remote, transversely oriented, the insertion subtransverse in dorsal half, the ventral half quite succubously oblique, with bistratose fields with abaxially projecting cells, and then the leaf lamina mamillose in profile, the leaves concave and loosely semiamplexicaul, often weakly sheathing basally, broadly ovate to quadrate-ovate, small, bifid to ca. 0.45–0.55; lobes erect, medium to rather broadly acute, with margins straight to at times arched, the lobes at times short-apiculate; sinus rather sharply V-shaped; lamina margins entire to sparingly dentate. Cells with walls thin to ± thickened, with trigones distinct, concave-sided, those of lobe margins and lobe apices ca. 12–15 μm to 14–17 μm wide, those of leaf middle small, ca. 13–15(17) × 13–18(20) μm, those of leaf base not or a little larger and hardly elongated; surface markedly coarsely papillose, with 2–6(8) coarse, contiguous-confluent, ± hemispherical hyaline papillae per cell surface, obscuring

cell outlines and content, the papillae ranging from 3–6 μm up to 5–6 × 5–9 μm in diam. Oil-bodies (Schuster, 1966c) 2–4(5) per cell, almost homogeneous, faintly granulate at best, glistening, ovoid to subspherical, large for the size of the cells (ca. 3–4 × 5 μm to 4.5–5.5 × 6–8[9] μm, in marginal and apical cells some only 2.5–3 × 3–4 μm). Underleaves consistently produced, 0.2–0.5× area of leaves, ovate to ovate-lanceolate, the apex at times bidentate; ventral merophytes relatively broad. Asexual reproduction lacking.

?Dioecious. Androecia not seen. Gynoecia terminal on leading shoots, with 1(2) subfloral innovations, at least if sporophytes are not produced; bracts of innermost series ovate-rotundate to oblate, bifid to 0.35–0.45, rarely trifid, the lobes ± divergent, medium to very broad acute, sometimes acuminate, at times with subparallel sides, the lobe margins sparingly dentate to coarsely spinose-dentate, the teeth sharp, irregular and jagged, the lamina margins dentate to spinose-dentate; cells of bracts coarsely papillose; bracteole oblong, bifid 0.3–0.35(0.45), the margins as in bracts. Perianth 0.5–0.65 emergent, ± inflated, obovoid, terete below, the distal third with 4–5 inflated, rounded plicae, contracted in distal 0.15; mouth lobulate, the lobules narrow, dentate to ciliate, the cilia hyaline, with a uniseriate row of up to 4 cells; perianth unistratose.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (ca. 1370–1495 m).

The type was collected in the alpine zone in the Sealy Ra. (Mt. Cook Natl. Park), over moist soil between rocks and associated with *Acrolophozia pectinata*, *Diplophyllum domesticum*, *Gymnomitrion denticulatum* and *Andreaea*. Not known from any other specimens.

Comments: This species differs from *Andrewsianthus cuspidatus* in the much larger underleaves, the rough and irregular stem surface with conical to finger-like cellular outgrowths, the much less sharply differentiated stem cortical cells, the smaller leaves and the stouter stem.

Subg. ***Andrewsianthus***

Andrewsianthus perigonialis (Hook.f. & Taylor) R.M.Schust.

[Fig. 150: 4, 6, oil-bodies, p. 684]

Jungermannia perigonialis Hook.f. & Taylor, London J. Bot. 3: 368. 1844. *Sarcoscyphus perigonialis* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 618. 1846. *Nardia perigonialis* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 401. 1877. *Sphenolobus perigonialis* (Hook.f. & Taylor) Berggr., New Zealand Hepat. 1: 22. 1898. *Lophozia perigonialis* (Hook.f. & Taylor) Grolle, Rev. Bryol. Lichénol. 31: 155. 1962. *Andrewsianthus perigonialis* (Hook.f. & Taylor) R.M.Schust., Rev. Bryol. Lichénol. 34: 281. 1966. Type: Auckland Is.

Plants rather wiry, green, tinted brown to chestnut-brown, the leafy shoots to 840 μm wide, at least sporadically becoming flagelliform and geotropic. Branching frequent, the branches lateral-intercalary, *Andrewsianthus*-type branches present, the leafy shoots arising from a system of plagiotropic, microphyllous, arcuate axes; ventral-intercalary branches occasional, from leafy shoots, the branches stoloniform and geotropic; stoloniform, microphyllous shoots sometimes predominant in some populations. Stems rigid, the cortex in 1–2 layers of thick-walled cells smaller than those of the medullary. Leaves vertical, stiffly obliquely to widely spread-

ing, only slightly dorsally assurgent, remote, transversely oriented, the insertion nearly transverse dorsally, quite succubous elsewhere, the lines of insertion extending to stem midline dorsally; leaves somewhat concave, ovate to oblong-ovate, subsymmetric to ± symmetric, the ventral margin at times a little more strongly arched than the dorsal, the dorsal and ventral leaf bases not dilated, so that the leaf bases do not extend beyond the stem midline, the leaves 420–700 μm wide × 580–700 μm long, somewhat asymmetrically 0.15–0.2(0.25) bilobed, the ventral lobe larger; lobes mostly blunt, at times obtusely rounded; sinus obtuse, angular to crescentic. Cells with walls firm, with trigones large and bulging, often ± confluent, the marginal cells in lobes 13–18(20) μm wide, the median cells 15–18 × 18–25 μm, the basal cells are essentially identical in size and not distinctly longer; surface weakly striate-papillose. Oil-bodies occupying moderate to conspicuous portion of cell lumen, dull, pale smokey grey, 2–4 to 3–5(7) per median leaf cell, finely granular, no protrusion of the tiny spherules, the oil-bodies subglobose and 5–6.5 μm in diam. to broadly elliptic and 4–6.5 × 9–12 μm, often somewhat irregular. Underleaves completely lacking (ventral merophytes only ?1 cell broad, the lines of insertion extending nearly to stem midline ventrally). Asexual reproduction lacking.

Androecia terminal but becoming intercalary on leading leafy axes, laxly spicate, the bracts deeply concave-ventricose throughout. Gynoecial bracts of innermost series 3-lobed, often asymmetrically so, the lobe apices blunt, the margins entire, the lamina margins entire or the dorsal margin with a tooth; bracteole conspicuous, distinctly connate on one side (fused to ca. 0.45 bracteole length), bilobed, the lobe margins entire, the lamina margins entire or the free margin with a tooth. Perianth and sporophyte not seen.

Distribution and Ecology: New Zealand: Auckland Islands, Stewart Island (3–ca. 100 m), South Island (ca. 1200 m); Australia: Tasmania (McCarthy, 2003). There are a number of collections from the Auckland Islands, but only three from Rakiura EP, including one from Whenua Hou (on a rock outcrop in scrub above Sealers Bay) and one from Canterbury (Arthur's Pass) EP.

At Belltopper Falls on Stewart Island it is found on a thin layer of soil on vertical or slightly overhanging bedrock surfaces only 3 m from the waterfall's edge and about 10 m from the sea, at a site kept constantly damp by spray from the falls, with *Hymenophyllum armstrongii*, *Drepanolejeunea aucklandica* and *Lepidozia kirkii*. Regenerating *Weinmannia racemosa* forest partially shades the site. At Otira Valley Track (Arthur's Pass Natl. Park, Canterbury, ca. 1200 m) plants occurred in a very tight mat comprised of *Jamesoniella colorata* and a filmy fern on the vertical face of bedrock near the top of a steep-sided knoll that had predominantly tussock-covered slopes with *Ranunculus* sp. and *Chionochloa* sp. and bryophyte-covered banks.

Comments: The shallowly bilobed leaves, divided to at most 0.2, the blunt to narrowly rounded leaf lobes, the weakly striate-papillose leaf surface and the absence of underleaves will separate this species from other New Zealand members of the genus.

Uncertain Species

Andrewsianthus confusus (R.M.Schust.) R.M.Schust.

Eremonotus confusus R.M.Schust., J. Hattori Bot. Lab. 26: 279. 1963 [based on *Sphenolobus perigonialis sensu* Steph., Sp. Hepat. 2: 163. 1902, *non Jungermannia perigonialis* Hook.f. &

Taylor]. *Andrewsianthus confusus* (R.M.Schust.) R.M.Schust., Rev. Bryol. Lichénol. 34: 281. 1966. Type: New Zealand, Stewart Is., 0.8–1.5 mi. above Port Pegasus, Pegasus Creek, *Schuster 49581*.

Schuster (1963b) validly published the name *Eremonotus confusus* R.M.Schust. by referring to Stephani's (1902) description of *Sphenolobus perigonialis*, and in so doing in a sense excluded the type of *S. perigonialis*. Schuster (1963b, p. 279) stated, "The plant described by Hodgson (1946) and by Stephani (Sp. Hepat. 2: 163. 1902), as '*Sphenolobus perigonialis*' is *not* identical [to *Anastrophyllum minutum*]; I have found this taxon on Stewart Is. (Pegasus Cr., *RMS 49581*). It appears undescribed; for it I propose the name *Eremonotus* (*Acantholobus*) *confusus*, with *RMS 49581* as type, and cite the Stephani diagnosis to validate it." Schuster (1968b, p. 489) added "*A. confusus* (R.M.Schust.) R.M.Schust. was, initially, legitimately validated by the citing of the unusually adequate Latin diagnosis in Stephani (1898–1924), for the simple reason that Stephani's diagnosis was based solely on the plant illustrated and described by Berggren (1898) as '*Sphenolobus perigonialis*,' nec *J. perigonialis* Hook.f. & Taylor = *Eremonotus confusus* R.M.Schust." Schuster (1968b) provided a synonymy and diagnosis (in both Latin and English) of *A. confusus*, and described the leaf sinus as descending to ca. 0.15–0.25, the leaf lobes as acute, and stated (p. 491) "the cuticle (*RMS 67-460*) is coarsely, confluently papillose to papillose-striolate." The lobe shape and leaf surface characters fit *A. cuspidatus*. The sinus depth, of ca. 0.15–0.25, is slightly shallower than we would allow for the species; we have studied a number of specimens ranging from Stewart Island to North Island, and we have found a sinus depth ranging from 0.2 to 0.4(0.55). Of interest is the collection number cited by Schuster (1968b) for the cuticle character (*RMS 67-460*), since this matches the collection number for a portion of fig. 335 (p. 330) of *A. cuspidatus* in Schuster (2002a).

The name *Andrewsianthus confusus* was used by Schuster (1966c, 1968b), but subsequently seems to have been abandoned in the literature. The name is not mentioned in Schuster's (2002a) overview of *Andrewsianthus* (pp. 320–339). If *A. confusus* is found to be conspecific with *A. cuspidatus*, the former would be the correct name for this plant. The two species are probably identical, but without examination of the types of *A. confusus* or *A. cuspidatus*, we do not wish to make a formal statement of synonymy. Hodgson (1967) included *Eremonotus confusus* in the synonymy of *Lophozia perigonialis*.

Subfam. ***Jungermannioideae***

Solenostoma Mitt.

Solenostoma Mitt., J. Linn. Soc., Bot. 8: 51. 1865, *nom. cons.*

Plants mostly erect or ascending (at least with crowding), deep green but, in sun, locally brownish purple to vinaceous to reddish (at least at ventral leaf bases), usually medium-sized and 550–1500 μm wide or more. Branching usually limited to older regions, the branches virtually always intercalary, from lateral leaf axils, often displaced to, or near to, ventral end of leaf insertion, the branches ascending, soon becoming normally leaved, or geotropic, rhizoidous and leafless; *Frullania*-type branches present in a few taxa, rare. Stems with cortex often ± distinct, 1(2)-layered, of weakly firm-walled cells, or sometimes of thinner-walled cells forming a hyaloderm; medullary cells thin-walled, infrequently firm-walled, more elongated than the cortical, lacking mycorrhizal infection. Leaves laterally ± spreading, alternate, the insertion usually succubous, but the dorsal end sometimes subtransverse, the lines of insertion extending to stem midline dorsally; leaves unlobed, edentate, ovate to orbicular, the

dorsal base usually ± decurrent. Cells thin-walled, with trigones usually distinct, small to somewhat nodose, the cells medium-sized; surface smooth or with distinct, rounded to elliptical to welt-like papillae. Oil-bodies several per cell, granular to very finely papillose, rather large. Underleaves wholly lacking, even in and near gynoecia. Asexual reproduction absent.

Dioecious or paroecious. Androecia intercalary with age, the bracts typically in several to many pairs, similar to leaves but more concave, at least toward the base, unlobed; antheridia usually (1)2–3 per bract, the stalk biseriate. Gynoecia nearly uniformly with a vestigial, low or high ring-like or tubular *Isotachis*-type perigynium lying in the axis of the stem, at least 1 bract inserted on the perigynium; bracts variable, their shape reflecting that of leaves; bracteole completely lacking. Perianth varying from long-emergent to abbreviated and included within the bracts, cylindrical to clavate, plicate (often 4-plicate) at least distally, the dorsal face of perianth not longitudinally sulcate, the perianth narrowed to mouth, with a beak absent, or if present, then the rostellum never depressed and situated at the truncate apex of the perianth; perianth mouth often crenulate by cells that are free for varying distances at their distal ends, the mouth cells often somewhat elongate.

Capsule subglobose to short-ellipsoidal, often irregularly splitting into 5–6 valves, wall 2- varying to 3- or 4(locally 5)-stratose; outer layer of cells with prominent nodular thickenings; inner layer of cells with semiannular bands, the bands usually complete.

Spores with low, delicate, fine papillae and short-vermiculate markings. Elaters tortuous, bispiral, the ends often thick-walled and nonspiral for varying lengths, the spirals only occasionally extending to elater tips.

Lectotype (Amakawa, 1960): *Solenostoma tersum* (Nees) Mitt.(≡ *Jungermannia tersa* Nees)

Schuster (2002a, p. 373) stated that *Solenostoma* "differs from *Jungermannia s. str.* in several not absolute ways: (a) *Solenostoma* species almost all develop a low, ring-like to distinctly tubular *Isotachis*-type perigynium subsequent to fertilization of the gynoecium (at least one ♀ bract is inserted on this); *Jungermannia* has only a simple, long-emergent perianth; bracts are inserted below the perianth base. (b) *Solenostoma* almost always develops reddish or vinaceous pigments, at least at ventral leaf bases, usually even in the shade; *Jungermannia* develops only brown to fuscous pigments. (c) *Solenostoma* species almost all show only lateral-intercalary branching [a few develop, rarely, isolated *Frullania*-type branches]; in *Jungermannia* terminal, *Frullania*-type branching is usually commonly developed." Also, "*Jungermannia s. str.* is chiefly a Laurasian genus, with almost all taxa in boreal to Arctic regions. By contrast, *Solenostoma* is virtually cosmopolitan in range..."

We are following, for several reasons, Schuster (2002a) in the recognition of *Solenostoma* as distinct from *Jungermannia*. *Jungermannia* in the broad sense is a "monster genus" (Schuster, 2002a, p. 373), and reduction of the size and circumscription of this and other very large genera makes them less unwieldy and generic limits easier to test. The segregate, smaller units are far easier to deal with in the way of testing differentiating taxonomic characters and assessment of phytogeographical patterns and ecological parameters. The two genera should be subjected to molecular studies prior to a conclusion that they should be treated as congeneric.

Southern temperate species are *Solenostoma crassulum* (Nees & Mont.) Steph. of Tristan da Cunha, Inaccessible Island, Gough Island, Falkland Islands, southern South America and Juan Fernandez, and six species from our area. These seven species belong to subg. *Solenostoma*. Two species of subg. *Plectocolea* Mitt. occur in Chile, *S. callithrix* (Lindenb. & Gottsche)

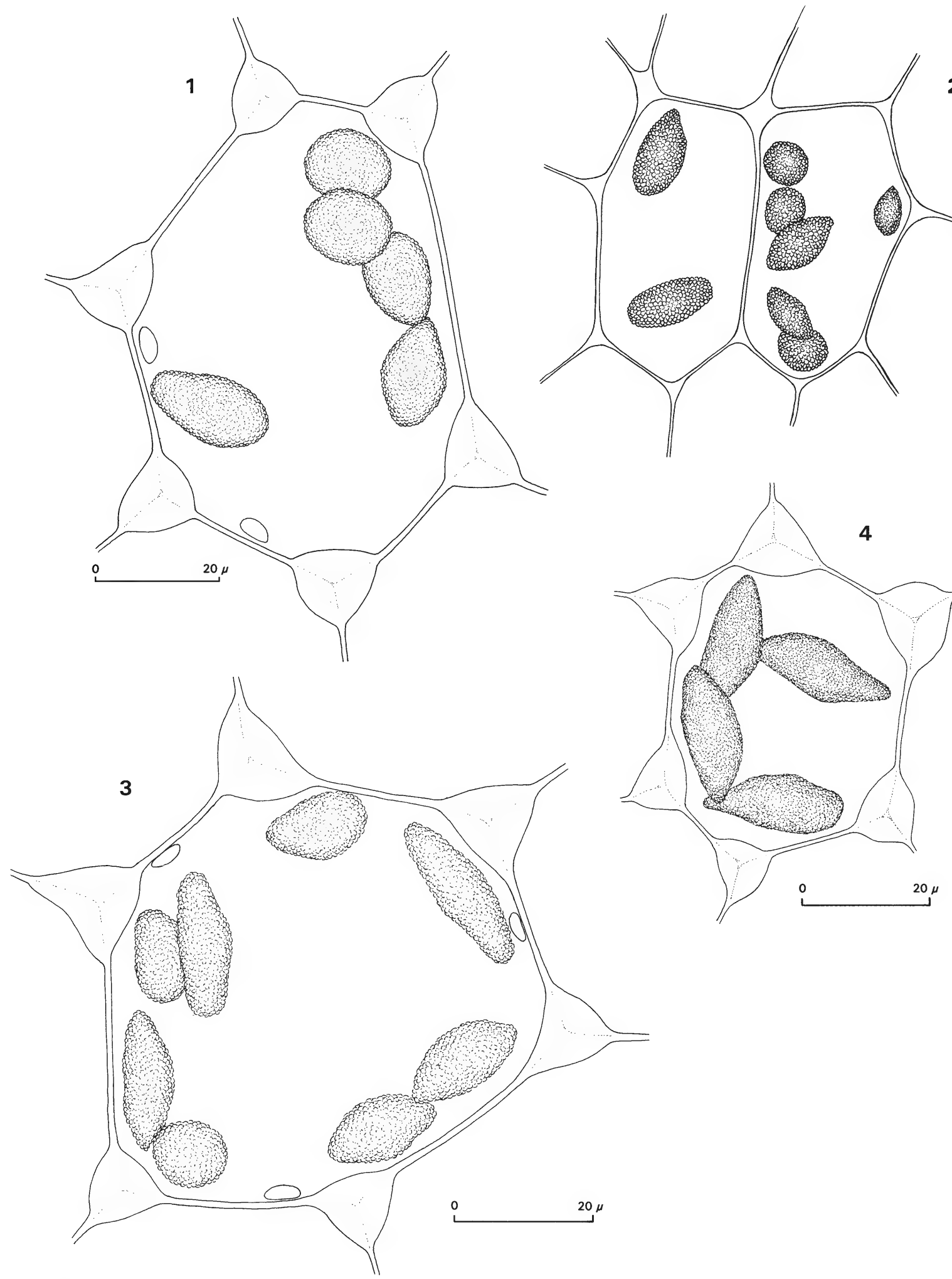

Fig. 151.
Oil-bodies. 1. *Solenostoma hodgsoniae* (Grolle) J.J.Engel. Median leaf cell, the outline of a few chloroplasts included. 2. *Solenostoma orbiculatum* (Colenso) R.M.Schust. (× 775). Median leaf cells. 3. *Solenostoma cryptogynum* R.M.Schust. *ex* J.J.Engel. Median leaf cell, the outline of a few chloroplasts included. 4. *Solenostoma cryptogynum* R.M.Schust. *ex* J.J.Engel. Median leaf cell. (Fig. 1, from *Engel 24777*, New Zealand, Westland EP, Cascade Road, just W of Jackson R.; 2, from

Steph., which also occurs in Ecuador, Venezuela north to Mexico and the Antilles, and *S. decolor* (Schiffn.) R.M.Schust., a species also found in Brazil, Ecuador and Venezuela.

According to Schuster (2002a), *Jungermannia* L. *s. str.* has seven to eight species, which are, with minor exceptions, all northern. Exceptions are *J. ovato-trigona* (Steph.) Grolle, which occurs in the Andes, and the Holarctic *J. pumila* With., which also is known from Tanzania, Lesotho and Natal.

References: Schuster (2002a); Váňa (1975).

Key to *Solenostoma* in New Zealand

1a. Plants minute (shoots 1 mm wide or less), often strongly reddish pigmented (or if green, then the leaves coarsely papillose). Capsule wall 2-stratose 2
- 2a. Leaf surface coarsely papillose, the papillae high and rounded (guttulate), (5)7–12 μm in diam., 3–8(10) per cell in distal portion of leaf; cortical cells of stem in surface view narrowly rectangular, the walls often thick and with the cell outlines obscure, often coarsely papillose like leaves; plants light green to brownish green or tinged with red; perianth turbinate, bluntly angled above, with a collar-like beak . . . . . *S. totipapillosum* (p. 711)
- 2b. Leaf surface indistinct to coarsely papillose (but not guttulate), the papillae low, 4–5 μm in diam., 10–15 per cell; cortical cells of stem in surface view large, quadrate, the walls thin and sharply defined, the surface smooth to finely papillose; plants typically reddish brown to deep wine-red; perianth elliptic, plicate, tapering to an indistinct beak . . . . . *S. rufiflorum* (p. 709)

1b. Plants small to large to robust (to 5 mm wide), grass-green to brownish green (exceptionally reddish tinged) 3
- 3a. Plants small, erect to ascending; rhizoids sparsely developed; leaves erect-spreading, not dorsally assurgent; leaf cells 24–27 μm wide, the walls moderately and ± evenly thickened, with small, straight-sided trigones. Surface finely striolate or almost smooth . . . . . *S. inundatum* (p. 707)
- 3b. Plants medium to large, prostrate to erect and densely caespitose; rhizoids abundant, from ventral surface of stem; leaves dorsally assurgent and bilaterally appressed (at least when dry); leaf cells 28–60 μm wide, ± thin-walled, with sharply distinct, small to large and bulging trigones 4
  - 4a. Shoots medium, to 3 mm wide; leaves broadly elliptic to orbicular, to 2 mm wide; leaves subtransversely to moderately succubously inserted, the dorsal margin not strongly decurrent; leaf cells in distal sector at most 46 μm wide and long; leaf surface striolate-papillose; capsule wall 2–3(locally 4)-stratose; antheridial stalk biseriate 5
    - 5a. Perianths when young inflated, not laterally compressed, at maturity long-exserted beyond bracts; leaves succubously oriented, the dorsal

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Engel 22656, New Zealand, North Is., Northland EP, Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge; 3, from *Glenny 9417*, New Zealand, South Is., Western Nelson EP, Reefton, Awarau R.; 4, from *Glenny 9096*, New Zealand, South Is., Westland EP, Lake Kaniere Road.)

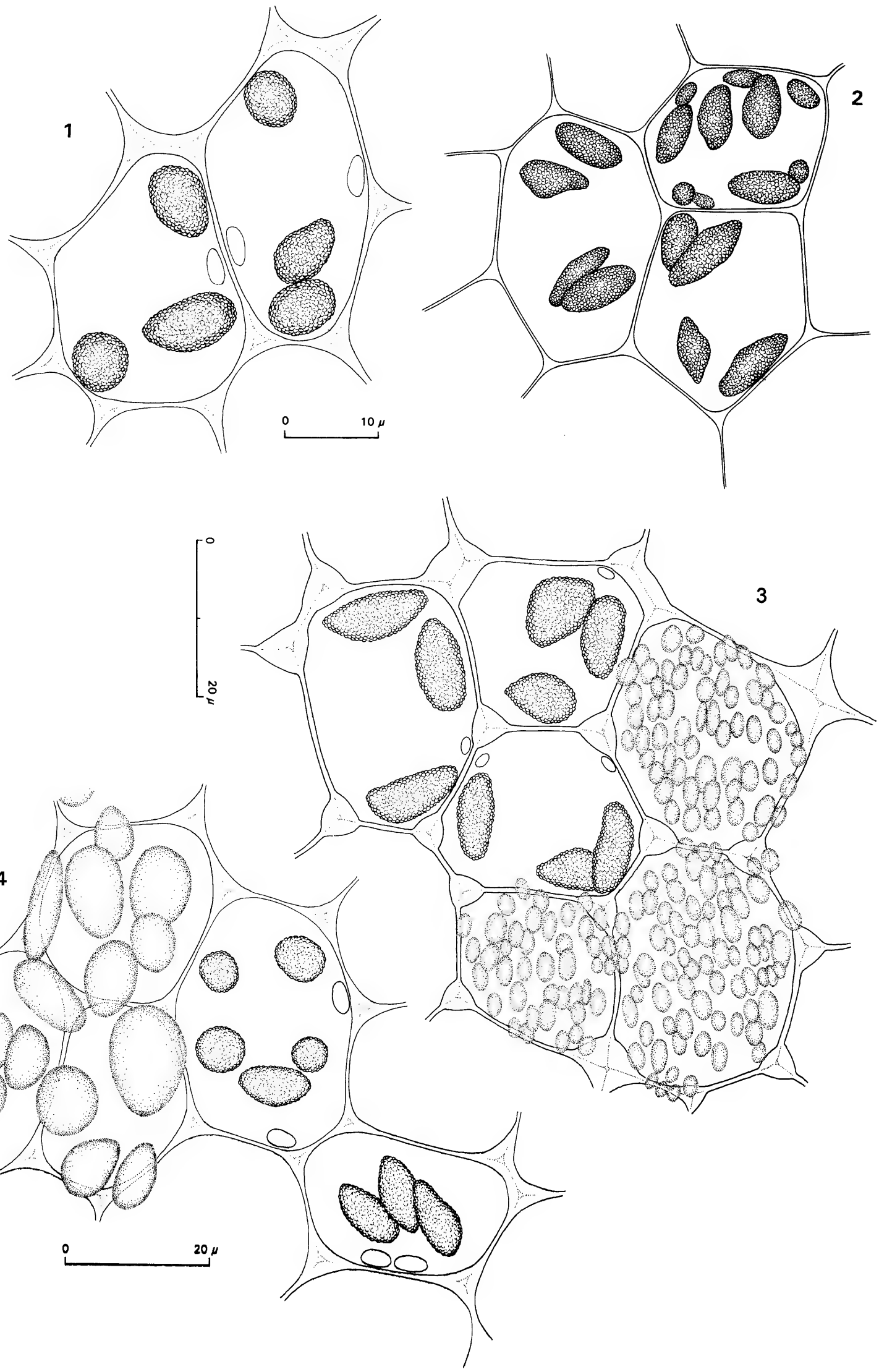

Fig. 152.
Oil-bodies, all (except fig. 2) with the outline of a few chloroplasts included. 1. *Solenostoma inundatum* (Hook.f. & Taylor) Mitt. *ex* Steph. Median leaf cells. 2. *Solenostoma inundatum* (Hook.f. &

and ventral margins short-decurrent; median cells (27)30–43(48) μm wide × 41–48(55) μm long, the cells in distal sector isodiametric, 28–33 μm wide and long . . . . . *S. orbiculatum* (p. 703)

5b. Perianths when young, laterally compressed, at maturity included with bracts; leaves subtransversely oriented, the dorsal and ventral margins not decurrent; median cells 46–61 μm wide × 50–72 μm long, the cells in distal sector isodiametric, 35–46 μm wide and long . . . . . *S. cryptogynum* (p. 705)

4b. Shoots robust, to 5 mm wide; leaves reniform, to 3.5(5) mm wide; leaves ± longitudinally inserted, the dorsal margin distinctly decurrent; leaf cells in distal sector 50–60 μm wide and long; leaf surface smooth; capsule wall 4(locally 5)-stratose; antheridial stalk polyseriate . . . . *S. hodgsoniae* (p. 699)

Solenostoma hodgsoniae (Grolle) J.J.Engel

[Plate 13F, G; Fig. 151: 1, oil-bodies, p. 696; Figs. 153, 154]

Jungermannia hodgsoniae Grolle, Bot. Mag., Tokyo 78: 83. 1965, *nom. nov. pro Lethocolea grandifolia* Berggr., New Zealand Hepat. 1: 26. *f. 19*. 1898. *Symphyomitra grandifolia* (Berggr.) Steph., Sp. Hepat. 2: 107. 1901. *Jungermannia grandifolia* (Berggr.) E.A.Hodgs., Trans. Roy. Soc. New Zealand 85: 582. 1958, *non J. grandifolia* Hook.f. & Taylor, London J. Bot. 3: 474. 1844 (= *Leptoscyphus horizontalis* (Hook.) Kuhnem.). *Solenostoma hodgsoniae* (Grolle) J.J.Engel, Novon 17: 312. 2007. Lectotype (*fide* Váňa, 1975): New Zealand, South Is., Westland Prov., Teremakau River, between Blake's and Kelly's, Mar. 1874, *Berggren 3140* (LD, *non vidi*); isolectotype: (G!).

Plants mostly strongly prostrate, rarely ascending, tightly adhering to substrate and to other shoots laterally and below by abundant rhizoids and often forming tight, compact groups of several individuals or small mats, often appearing turgid and julaceous, usually bright grass-green to yellowish green, less often brownish green, often strongly tinged with clear wine-red at bases of leaves, the plants robust for genus, to 5 mm wide, the shoot tips rather abruptly turned upward. Branching infrequent, lateral-intercalary. Stems thick and fleshy, colorless to brownish green to rose-tinted, the cortex of 1 (locally 2) rows of much smaller cells; medullary cells large, thin-walled. Rhizoids long, abundant, diffuse, never in bundles, arising from the ventral side of stem and from extreme bases of leaves, colorless to yellowish, the surface indistinctly roughened. Leaves horizontally laxly spreading to more commonly dorsally assurgent, the dorsal margins (seen on edge in dorsal view) vertically oriented and mutually appressed along the median line, the leaves weakly concave, the median basal portion of the leaf

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Taylor) Mitt. (× 875). Median leaf cells. 3. *Solenostoma rufiflorum* (Colenso) J.J.Engel. Upper-median leaf cells; note that papillose surface is shown for 3 cells. 4. *Solenostoma totipapillosum* (E.A.Hodgs.) R.M.Schust. Median leaf cells; note that papillose surface is shown at left. (Fig. 1, from *Glenny 9115*, New Zealand, South Is., Westland EP, Upper Otira Valley; 2, from *Engel 22439*, New Zealand, North Is., Wellington, Tongariro Natl. Park, Taranaki Falls Track; 3, from *Glenny 9693*, New Zealand, South Is., Westland EP, Dickie Ridge; 4, from *Glenny 9291*, New Zealand, South Is., Western Nelson EP, Moonlight Creek.)

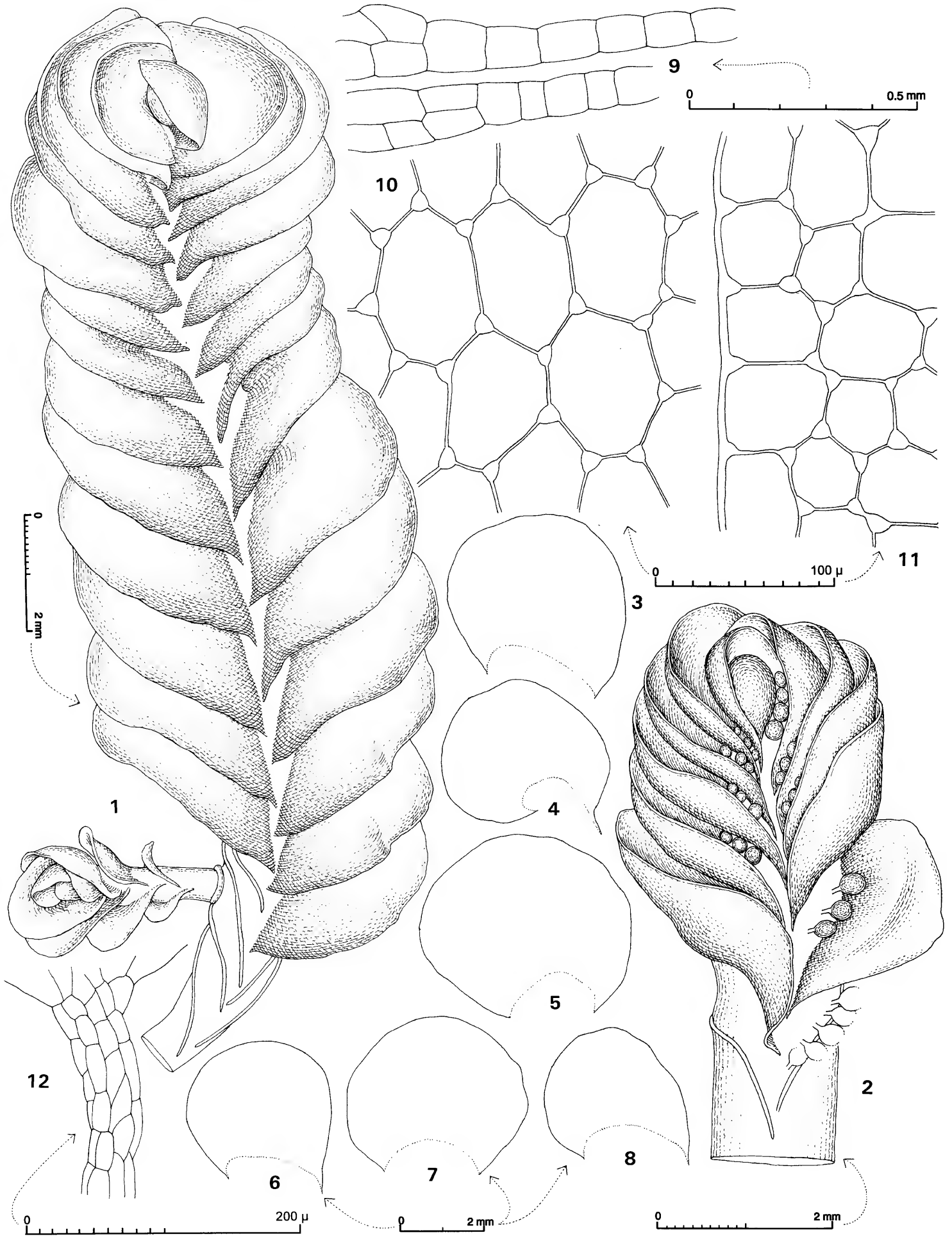

Fig. 153.
Solenostoma hodgsoniae (Grolle) J.J.Engel. 1. Shoot with lateral-intercalary branch at lower left, dorsal view. 2. Androecial-bearing shoot. 3–8. Leaves (all drawn to same scale). 9. Longitudinal section through basal sector of 2 leaves (the base at left). 10. Median leaf cells. 11. Sector of leaf apex. 12. Antheridial stalk. (Figs. 1, 3–8, 10, 11, from *Engel 21152*, New Zealand, South Is., Western Nelson EP, track to German Terrace, 6 km SSE of Westport on Nine Mile Road, 90 m; 2, 12, from *Braggins 84/400A*, New Zealand, North Is., Wellington, Akatarawa; 9, from *Engel 25036*, New Zealand, South Is., Western Nelson EP, Mt. Arthur, Mt. Arthur Hut track, 1050–1250 m.)

concave and laxly sheathing the stem, the insertion steeply oblique to ± longitudinal for most of its length, abruptly short-recurved at ventral end; leaves 2–3-stratose in median-basal sector, orbicular to reniform (when flattened), broader than long, to 2.5–4(5) mm wide, 2–3 mm long, entire, the apex broadly rounded, the margins sometimes undulate, the dorsal moderately to distinctly decurrent, the ventral abruptly short-decurrent. Cells thin-walled, with sharply defined, small, straight-sided to bulging to at times knot-like trigones, the cells of median portion of leaf lax, short-rectangular, 38–54 μm wide × 55–78 μm long to ± inflated, 50–84(96) μm wide × 72–98(125) μm long, the cells in distal sector smaller, ± isodiametric to somewhat broader than long, (30)50–60 μm wide and long, the marginal cells 37–48 μm wide and long; surface smooth. Oil-bodies pale greyish brown, (2)3–5(7) per cell, moderately granular, the spherules not protruding beyond membrane, the oil-bodies subglobose to ovoid to elliptic. Underleaves absent. Asexual reproduction absent.

Dioecious. Androecia terminal and rosette-like, becoming intercalary; bracts very little differentiated from the leaves, broadly overlapping, in 3–6 pairs, concave, widely spreading, the antheridia often plainly visible from above, 3–4(5) per bract, the stalk polyseriate. Gynoecia terminal but appearing sessile on dorsal side of shoot, the shoot continuing growth by a stout intercalary innovation, with ca. 2–3 series of bracts that gradually merge in size and form with leaves, bracts of innermost series weakly united with the base of the perianth, the bracts broadly reniform, with a truncate apex, similar to the vegetative leaves in shape but larger; bracteole absent. Perianth not exserted beyond bracts, the summit of the beak at about the same level as the bract margin, the perianth ovate to ellipsoid, distinctly 5-plicate, abruptly constricted at the mouth, short-beaked, the mouth ± regularly crenulate by projecting cells that arch inward; cells of beak portion elongated, uniformly slightly thick-walled, those at mouth with tips often free for up to ca. 0.5 (occasionally free for greater distances), bluntly rounded at the summit; cells of the perianth proper similar to the leaf cells in form and size, with large trigones.

Seta seen only in collapsed state. Capsule irregularly splitting into ca. 6 valves, the walls carmine red, the wall 4(locally 5)-stratose, 62–67 μm thick, the outer layer a little less than subequal to the thickness of all inner layers combined; outer layer of cells subquadrate to short-rectangular, thin-walled, with prominent deep carmine to almost blackish nodule-like to short spine-like thickenings on most longitudinal walls, the transverse walls often with similar thickenings; inner layer of irregularly elongated cells, the longitudinal walls with thin, sheet-like, pigmented thickenings and narrow, often semiannular bands, the bands sporadically branched.

Spores with walls thin, very pale brown, 15.8–19.2 μm in diam., with low, delicate, fine papillae and short-vermiculate markings. Elaters tortuous, 9.6–10.6 μm wide, bispiral, the ends thick-walled and nonspiral for ca. 0.25–0.35 the elater length, the thick-walled portion ± parallel-sided and sinuous, the spirals 3.8–4.3 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (15–1250 m). Known only from Westland and Western Nelson EPs.

Occurring on large vertical, stabilized, clayey banks at roadsides, at times at the upper extremity of the bank at the lip of forest. For example, at Cascade Road (just W of Jackson River, SW of confluence of Jackson and Arawata rivers, Westland, 45 m) it occurs on bryophyte-covered roadside banks dominated by *Isotachis*, with *Fuchsia excorticata* at the base of the bank (at the margin of a mature *Nothofagus menziesii* forest). Also on vertical banks along tracks, e.g., along the track to German Terrace (SSE of Westport on Nine Mile Road, 90 m) at the margin of a forest of *N. truncata*. At Mt. Arthur Hut Track (Kahurangi Natl. Park) occur-

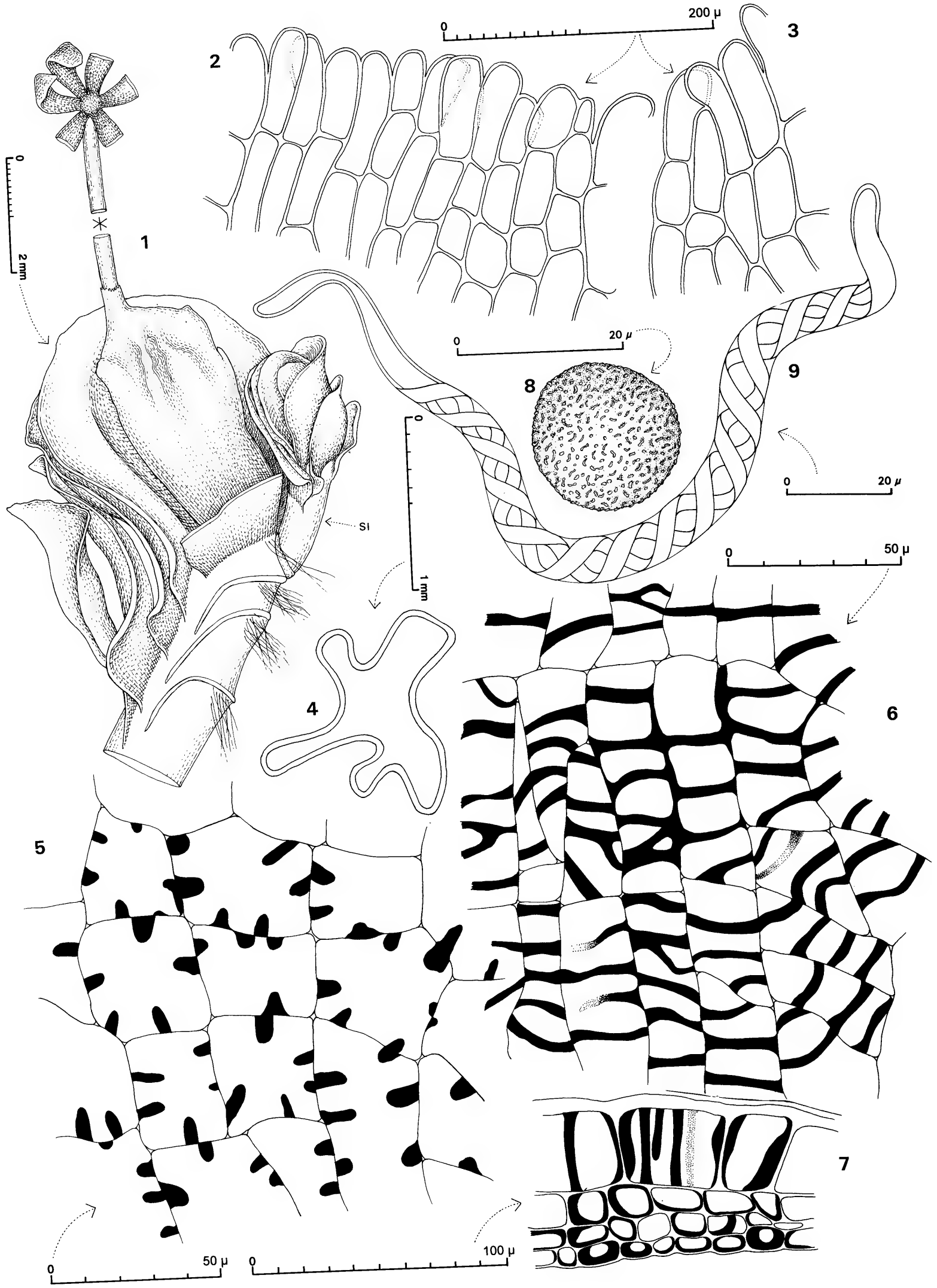

Fig. 154.
Solenostoma hodgsoniae (Grolle) J.J.Engel. 1. Shoot apex with mature sporophyte, dorsal-lateral view (SI = subfloral intercalary innovation; the innermost bracts on near side removed for clarity). 2, 3. Portions of perianth beak. 4. Perianth, cross section through median sector. 5. Capsule wall,

ring at 1050–1250 m over thick soil in a crevice at the side of a sinkhole in a *N. menziesii* forest. Exceptionally on vertical clayey banks in the penalpine zone, e.g., in an area dominated by *Dracophyllum* and *Olearia* at 1150–1170 m along the track to Alex Knob (Westland Natl. Park). Plants typically occur prostrate over soil as pure small mats or, less often, admixed among other bryophytes; shoots tightly adhere to the substrate and to other shoots of the species. It has been found with *Cryptochila nigrescens*, *Hypnum chrysogaster*, *Isotachis montana*, *Lembidium longifolium*, *Lepidozia spinosissima*, *Pallavicinia tenuinervis*, *Pohlia wahlenbergii* and *Telaranea tetrapila*.

Comments: *Solenostoma hodgsoniae* is a striking plant, with its broad, grass-green shoots, growing prostrate and firmly adhering to the substrate by the copiously developed rhizoids arising from the ventral side of the shoot. The leaves are broadly orbicular to reniform and overlap broadly at the shoot tips forming conspicuous, flaring rosettes. Although the plant is typically an intense green in color, the leaf bases are often rose-tinted.

Váňa (1975) treats *Solenostoma hodgsoniae* as a "mod. *leptoderma-magnifolia*" of *S. orbiculatum* (p. 703), but as circumscribed here, *S. orbiculatum* is abundantly distinct in its smaller size, more compact leaf areolation and striolate surface. The size of *S. hodgsoniae* alone (shoots to 5 mm wide) distinguishes it from any other New Zealand member of the genus. See also comments under *S. orbiculatum*.

Solenostoma orbiculatum (Colenso) R.M.Schust.

[Fig. 151: 2, oil-bodies, p. 696]

Gymnomitrion orbiculatum Colenso, Trans. & Proc. New Zealand Inst. 18: 236. 1886 ("*Gymnomitrium orbiculata*"). *Jungermannia orbiculata* (Colenso) Grolle, J. Jap. Bot. 4: 144. 1966, *non J. orbiculata* (Amakawa) Amakawa, J. Hattori Bot. Lab. 30: 188. 1967 (= *J. suborbiculata* Amakawa). *Solenostoma orbiculatum* (Colenso) R.M.Schust., Beih. Nova Hedwigia 119: 380. 2002. Lectotype (*fide* Váňa, 1975): New Zealand, Waipawa Co., near Norsewood, Mangatawhainui River, Oct. 1884, *Colenso* (WELT, *non vidi*); probable isolectotype: (MPN, hb. Hodgson no. 13679, *non vidi*).

Jungermannia fragilis Gottsche, Linnaea 28: 551. 1857, *non J. fragilis* Roth, Tent. Fl. Germ. 3: 370. 1800. *Jamesoniella fragilis* Steph., Sp. Hepat. 2: 102. 1901. Lectotype (Váňa, 1975): Australia, "in alpibus australibus," *F. Müller*.

Solenostoma contexta Kaal. *ex* Steph., Sp. Hepat. 2: 56. 1901. Lectotype (Váňa, 1975): New Zealand, North Is., Taupo, Huka Falls, 1888, *Roper*.

Jungermannia cambewarrana Steph., Sp. Hepat. 6: 84. 1917. *Plectocolea cambewarrana* (Steph.) Herzog, Ark. Bot. 3(3): 49. 1955, *nom. inval.* Type: Australia, New South Wales, Cambewarra Pass, 1903, *Watts 898a*.

Plants prostrate or more commonly ascending to suberect in tightly interwoven mats, resembling *Solenostoma hodgsoniae* but smaller, often forming tight, closely spaced rosettes, bright green to yellowish to brownish green, rarely somewhat reddish, the plants medium-sized, to 2.5 mm wide. Branching common, the plants irregularly and often repeatedly branched, the

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outer layer. 6. Capsule wall, inner layer. 7. Capsule wall, cross section. 8. Spore. 9. Elater. (Figs. 1, 5–9, from *Braggins 84/400A*, New Zealand, North Is., Southern North Is. EP, Akatarawa; 2–4, from *Engel 21152*, New Zealand, South Is., Western Nelson EP, track to German Terrace, 6 km SSE of Westport on Nine Mile Road, 90 m.)

branches lateral-intercalary. Stem greenish to brownish green, the cortical cells indistinct, in a single layer of smaller cells; medullary cells lax, thin-walled. Rhizoids numerous, colorless to pale brownish, diffuse, never in bundles, arising from the ventral side of stem and from extreme bases of leaves, smooth. Leaves rather firm, vertically oriented, ± bilaterally appressed to the stem, loosely to closely imbricate, succubously oriented, the insertion variable, oblique in extreme dorsal portion, becoming subtransverse, abruptly reflexed at ventral end; leaves plane to concave, weakly asymmetric, elliptic-oval to oblate to subreniform, often broader than long, entire, 1.5–2 mm wide, 1–1.5 mm long, the apex broadly rounded or weakly emarginate; margins plane to distinctly reflexed, not undulate, the dorsal and ventral margins about equally short-decurrent. Cells thin-walled but not inflated, with small but prominent, bulging to knot-like trigones; cells of lower median sector of leaf larger, short-rectangular, (27)30–43(48) μm wide × 41–48(55) μm long, the cells in distal sector smaller, firm-walled, hexagonal, often somewhat wider than long, 28–33 μm wide and long, the marginal cells almost isodiametric, 20–27 μm in diam.; surface closely striolate-papillose (at least in median basal sector). Oil-bodies very pale grey, (2)3–6 per cell, finely granular, the spherules very slightly protruding beyond membrane, the oil-bodies elliptic to fusiform to spherical, 5.9–7.8 × 15.6–16.6 μm, some 4.9–7.8 × 11.7–13.7 μm, spherical ones 6.8 μm in diam. Underleaves absent. Asexual reproduction absent. Fungal partner absent.

Dioecious. Androecia terminal, rarely becoming intercalary, inconspicuous; bracts very little differentiated from the leaves, in 3–8 pairs, transversely inserted, widely spreading, the margins recurved, the basal portion moderately concave; antheridia 2–3 per bract, the stalk biseriate. Gynoecia terminal, typically with several lateral-intercalary innovations at some distance below the gynoecium, the subinvolucral leaves gradually larger, the bracts broadly reniform, weakly united with the base of the perianth; bracteole absent. Perianth ca. 0.5 immersed, inflated, ellipsoid, ± irregularly and sharply plicate in distal 0.3–0.5, often with short, irregular accessory ribs and scabrous near the apex, the mouth contracted to a short beak, the mouth irregularly crenulate by projecting cells; cells of beak portion short-rectangular, uniformly thick-walled, their tips irregularly projecting; cells of the perianth proper isodiametric, firm-walled, with distinct trigones.

Capsule short-ellipsoidal, the wall 2–3-stratose, 40–48 μm thick, the outer layer equaling the 2 inner layers in thickness; outer layer of cells short-rectangular, thin-walled, with short peg-like thickenings on the longitudinal walls, sporadically extending a short distance onto the outer tangential wall, the transverse walls rarely with peg-like thickenings; innermost layer of cells with longitudinal walls with thin sheet-like thickenings and ± regular, rather narrow, complete scalariform bands.

Spores yellowish brown, 16.8–19.7 μm in diam., finely papillose, the papillae distinct or forming short, irregular vermiculate ridges that do not delimit areolae. Elaters 8.6–9.1 μm wide, bispiral, the ends long-tapering and sinuous, the spirals 2.9–3.8 μm wide, not extending into the elater tips.

Distribution and Ecology: New Zealand: Stewart Island (sea level), South Island (20–310 m), North Island (95–480 m); Australia: New South Wales. In New Zealand known from Southland, Otago, Westland and Southern North Island EPs.

A species primarily of relatively low elevations in the forest zone. On stream banks it occurs over thick soil on boulders submerged to periodically inundated, and in streambeds it occurs on the tops of rocks that are for the most part above water level. Also on moist, stabilized roadside banks that are covered mostly by hepatics, mosses, often also with *Blechnum* and the

lichen *Stereocaulon*. For example, at Cascade Road (just W of Jackson River, ca. 10 km SW of confluence of Jackson and Arawata rivers, Westland, 45 m) it occurred on a huge rock face of a large, vertical, bryophyte-covered roadside bank dominated by *Isotachis*, with *Fuchsia excorticata* at the base of the bank, the bank at the margin of a mature *Nothofagus menziesii* forest. Accompanying species on such banks are *Campylopus clavatus*, *Chiloscyphus mitteni-anus*, *C. subporosus*, *Isotachis montana*, *Pohlia wahlenbergii* and *Polytrichadelphus magellan-icus*. The species exceptionally is alpine, occurring, for example, at the top of a rock in a rill-bed at 1360–1480 m in a mosaic of tussockland and alpine vegetation along with tarns, rills, rocky outcrops and boulderfields (Rainbow Skifield, St. Arnaud Ra., Nelson Lakes Natl. Park). *Solenostoma inundatum* is much more frequent at upper elevations, including the alpine zone.

Comments: *Solenostoma orbiculatum* resembles *S. hodgsoniae* in the lack of strong pig-mentation, the shape and position of the leaves, and the prostrate habit and abundant rhizoids from the ventral side of the stem. Schuster (2002a) confused these species, referring to *S. orbic-ulatum* plants that are "vigorous" with "leaves to 3.0–3.6 mm × 3.3–4.1 mm" and a "capsule wall 4-layered" (key, p. 376), which match characters of *S. hodgsoniae*. Schuster (2002a) also illustrated these vigorous plants (figs. 353A, 354: 5–7, both as *S. orbiculatum*), and com-mented (p. 380) "this is one of the largest *Solenostoma* spp. known..." *Solenostoma orbicula-tum sensu* Schuster (2002a), then, is identical to *S. hodgsoniae*. *Solenostoma novaezelandiae* R.M.Schust. may be the same as *S. orbiculatum* (see under "Uncertain Species"). The true *S. orbiculatum* is a smaller plant, with smaller cells and more uniform areolation, and the sur-face is decidedly striate-papillose, vs. smooth in *S. hodgsoniae*. It differs from *S. inundatum* in its prostrate habit and more obliquely inserted, dorsally assurgent leaves.

Solenostoma cryptogynum R.M.Schust. *ex* J.J.Engel

[Plate 13B; Fig. 151: 3, 4, oil-bodies, p. 696]

Solenostoma cryptogynum R.M.Schust., Beih. Nova Hedwigia 119: 380, 381. *f. 355: 5–11, 356.* 2002, *nom. nud.* (*sin. descr. lat.*). *Solenostoma cryptogynum* R.M.Schust. *ex* J.J.Engel, Novon 17: 311. 2007. Holotype: New Zealand, North Is., South Auckland Prov., Whirinaki Forest Park, road to Arahaki Lagoon, SSW of Minginui, 380 m, *Engel 20730* (F); isotype: (CHR).

Plants spongy, prostrate to a little ascending, markedly brittle, resembling *Solenostoma or-biculatum* in general aspect, tightly adhering by abundant rhizoids to other shoots both later-ally and below and often forming compact, tight, pure, small mats, the shoots often appearing turgid, the shoots pure green or with stems and leaf bases light green and distal parts of leaves and perianths rusty red, the plants medium-sized, to 3 mm wide. Branching (vegetative) not seen. Stem with cortical cells moderately differentiated, in a single (locally 2) layer of smaller, thin-walled cells; medullary cells thin-walled. Rhizoids numerous, long for shoot size, color-less to pale brownish, diffuse, never in bundles, arising in a rather broad zone from the ventral side of stem and from extreme bases of leaves. Leaves rather rigid, firmly attached, semiver-tical, obliquely to widely spreading, those toward shoot apices tend to be suberect and shoot tips may be almost bivalved, densely imbricate, subtransversely oriented, the insertion oblique in ca. dorsal two thirds, becoming subtransverse in ventral third; leaves 2-stratose at extreme base in median sector, concave, subsymmetric, suborbicular to oblate to subreniform, often broader than long, entire, (1.7)2–3.2 mm wide, (1.5)1.8–2.8 mm long, the apex broadly rounded; dorsal margin plane, the ventral often sharply reflexed toward base, the dorsal and

ventral margins not decurrent. Cells thin-walled, with bulging, nodular trigones; cells of median sector of leaf not much longer than wide, 46–61 μm wide × 50–72 μm long, the cells in distal sector smaller, isodiametric, 35–46 μm wide and long; surface closely striolate-papillose (at least in median and basal sectors). Oil-bodies occupying small to moderate portion of cell, pale brownish or light chocolate-brown, (3)4–6(8) per median leaf cell, coarsely granular, broadly to long-elliptic to fusiform to subcrescentic to linear to paramecioid to potato-shaped, and less often short-elliptic, 9 × 11 μm to 8 × 17 μm to 7–9 × 24–30 μm. Underleaves absent, the ventral merophytes very narrow. Asexual reproduction absent.

Dioecious. Androecia terminal, inconspicuous; bracts hardly differentiated from the leaves, in 4–5 pairs, the margins plane to feebly recurved, the basal portion moderately concave; antheridia 4–5 per bract, the stalk biseriate. Gynoecia terminal, often with an innovation, the innovations ventral-intercalary, the subinvolucral leaves gradually larger, the bracts of innermost series reniform, the bracts in young gynoecia suberect and ± clasping the young perianth; bracteole absent. Perianth when young laterally compressed, with distinct dorsal and ventral keels, the mature perianths included with bracts or extending at most a little beyond, inflated, clavate, ± irregularly and sharply 5-plicate in distal ca. 0.5, the summit of each plica a ± sloping or truncate "shoulder," the mouth contracted to a distinct beak, the beak summit crenulate by cells that are somewhat elongate, uniformly thick-walled, and with their tips somewhat irregularly projecting, with sporophyte extrusion the beaked perianth apex becomes strongly fissured, the beak splitting into several tapered segments.

Seta seen only in collapsed state. Capsule irregularly splitting into ca. 6 valves, the wall carmine red, 3(locally 4)-stratose, 52–56 μm thick, the outer layer ca. 0.6 the total wall thickness; outer layer of cells subquadrate to short-rectangular, thin-walled, with prominent deep carmine to almost blackish nodule-like thickenings on most longitudinal walls and absent or few on transverse walls; inner layer of irregularly elongated cells, the longitudinal walls with very thin, evenly sheet-like, pigmented thickenings and narrow, usually complete semiannular bands, the bands not branched.

Spores pale red-brown, 15.8–18.2 μm in diam., with low, delicate, well-defined short-vermiculate markings that often branch and coalesce, the surface also with a few papillae. Elaters tortuous, 9.1 μm wide, bispiral, the ends thick-walled and nonspiral, the thick-walled portion ± parallel-sided, the spirals 3.8–4.8 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (100–500 m), North Island (380 m). Known only from Westland and Volcanic Plateau EPs, from a few collections, but likely will be found to be more common after study of specimens previously thought to be *Solenostoma orbiculatum*. At Whirinaki Forest Park, road to Arahaki Lagoon (Volcanic Plateau EP), plants occurred on soil over rock in thick *Leptospermum scoparium* scrub. In Westland, it has been found on the vertical edges of outwash and moraine terraces, on coarsely stony soils, under *Dacrydium cupressinum – Weinmannia racemosa* forest or *Nothofagus fusca* forest, or in the open adjacent to a river. It has been found at these sites with *Campylopus clavatus*, *C. spiniferus*, *Dibaeis arcuata*, *Isotachis lyallii*, *Nertera balfouriana* and *Pallavicinia xiphoides*.

Comments: The species is similar to *Solenostoma orbiculatum* in general appearance and, as mentioned above, specimens have probably been misdetermined as that species. The gynoecium of *S. cryptogynum* is quite different in that the perianths, when young, are laterally compressed and at maturity are included within the bracts vs. perianths that when young are inflated and

not laterally compressed, and at maturity are long-exserted beyond the bracts in *S. orbiculatum*. When sterile, plants of the two species may be distinguished by several characters. In *S. cryptogynum* the leaves are subtransversely oriented, with non-decurrent dorsal and ventral margins, and the median cells are 46–61 μm wide × 50–72 μm long vs. leaves that are succubously oriented, with the dorsal and ventral margins short-decurrent, and median cells (27)30–43(48) μm wide × 41–48(55) μm long in *S. orbiculatum*.

Plants of this species, like *Solenostoma hodgsoniae* and probably some of our other species, have a notable habit. Shoots tightly adhere by abundant rhizoids to other shoots in the same populations, both to living shoots that are ± lateral as well as to colorless, probably nonliving ones below. These colorless shoots, in turn, similarly adhere to other shoots laterally and below, the entire mass forming a tight, compact, thick, rather solid mat.

Solenostoma inundatum (Hook.f. & Taylor) Mitt. *ex* Steph.

[Fig. 152: 1, 2, oil-bodies, p. 698]

Jungermannia inundata Hook.f. & Taylor, London J. Bot. 3: 559. 1844. *Nardia inundata* (Hook.f. & Taylor) Steph., J. Linn. Soc. Bot. 29: 274. 1892. *Solenostoma inundatum* (Hook.f. & Taylor) Mitt. *ex* Steph., Sp. Hepat. 2: 52. 1901 ("*inundata*"). Type: New Zealand, (North Is., Bay of Islands, cf. Váňa, 1975, p. 300), *Hooker*, ex herb. Kew (G!).

Jungermannia paucifolia Colenso, Trans. & Proc. New Zealand Inst. 18: 237. 1886. Type: New Zealand, 1885, *Colenso*.

Jungermannia humilissima Colenso, Trans. & Proc. New Zealand Inst. 18: 236. 1886. Type: New Zealand, Waipawa Co., Mangatawhaiiti River, 1885, *Colenso*.

Jungermannia polycarpa Colenso, Trans. New Zealand Inst. 19: 280. 1887. Type: New Zealand, Waipawa Co., near Norsewood, 1885–86, *Colenso*.

Nardia patellata Berggr., New Zealand Hepat. 1: 6. *f. 5*. 1898. *Solenostoma patellata* (Berggr.) Steph., Sp. Hepat. 2: 60. 1901. Lectotype (*fide* Váňa, 1975): New Zealand, South Is., Prov. Otago, near Invercargill, June 1874, *Berggren 2878* (LD, *non vidi*); isolectotype: (G!).

Solenostoma brevissima Pearson, Univ. Calif. Publ. Bot. 10: 313. *tab. 88*. 1923. Type: New Zealand, North Is., Rotorua, Whakarewarewa, 1904, *Setchell No. 155*.

Aplozia victoriensis Bibby, Rev. Bryol. Lichénol. 23: 132. *f. 1*. 1954. *Jungermannia victoriensis* (Bibby) E.A.Hodgs., J. Roy. Soc. New Zealand 2: 112. 1972. Type: Australia, Victoria, between Mt. Ben Cairn and Mt. Donna Buang, 1400 m, 1953, *Ashton*.

Plants typically ascending, rarely prostrate, rather lax, in compact, thin tufts, pale green, yellow-green to brownish, or tinged with deep red to purplish red, to 1.5 mm wide. Branching ± frequent, lateral-intercalary. Stems greenish, yellow- to brownish green, or purplish red, the cortex in 1–2 layers; medullary cells larger, thin-walled. Rhizoids sparingly produced, colorless to somewhat yellowish, from the ventral side of the stem, dispersed, never in bundles. Leaves erect-appressed to obliquely spreading, imbricate to ± distant, the insertion almost transverse, the leaves plane or ± concave, elliptic to broadly ovate to orbicular, 840–910 μm wide × 700–720 μm long, the apex broadly rounded to weakly emarginate, the margins weakly recurved, the dorsal and ventral margins only weakly decurrent. Cells with small to medium straight-sided trigones, the cells almost isodiametric, firm, those of distal portion of leaf (18)20–22 μm wide × 24–27 μm long, the cells at the margins smaller, 18–24 μm wide; cells of basal 0.3 of leaf larger, to 38 μm wide × 45 μm long; surface finely striolate or almost smooth. Oil-bodies hyaline, 4–7(8) per cell, finely granular, the spherules not protruding

beyond outer membrane, the oil-bodies rather narrowly to broadly elliptic to fusiform, sporadically spherical, variable in size, most larger and 5.9–7.8 × 10.7–15.6 μm, a few smaller and 2.9–3.9 × 4.9–6.8 μm, spherical ones 3.9 μm in diam. Underleaves absent. Asexual reproduction absent.

Dioecious. Androecia terminal, becoming intercalary, with 4–5 pairs of rather distant, transversely inserted bracts, the bract margins broadly recurved; antheridia 1–2, the stalk biseriate. Gynoecia terminal, often with one or more lateral-intercalary innovations; bracts of innermost series somewhat larger than the stem leaves, broadly oval to suboblate, almost transversely inserted, weakly united to the perianth base. Perianth long-exserted, rather large for plant size, exceeding the bracts, green or at times reddish tinged or purplish red, cylindrical to narrowly obovate, when dry terete in basal 0.5, then narrowed to a wrinkled to deeply furrowed, ± twisted neck, when moist cylindrical to obovate and abruptly contracted to the mouth, with an inconspicuous beak, the perianth mouth crenulate by projecting, ± isodiametric cells, the cells at times appearing transversely divided, with evenly thickened walls; cells of the perianth proper ± isodiametric, similar to those of the leaves.

Seta in cross section with an outer layer of 21 cells surrounding an inner core of 15 cells. Capsule reddish brown, almost globose, the wall 2-stratose, 34–36 μm thick, the outer layer about 2× the thickness of the inner layer; outer layer of cells short-quadrate, thin-walled, with prominent short peg-like thickenings of the longitudinal walls, the transverse walls sporadically with peg-like thickenings; inner layer of elongated cells with longitudinal walls with thin, sheet-like, pigmented thickenings and regular, very narrow, complete scalariform thickenings.

Spores reddish brown, 12–18 μm in diam., papillose, the papillae mostly distinct or united into short ridges. Elaters 7.2–12 μm wide, bispiral, the ends tapering and sinuous, the tip portion 2.9–4.3 μm wide, the spirals 3.1–3.9 μm wide, not extending into the elater tips.

Distribution and Ecology: New Zealand: Campbell Island (50–180 m), Antipodes Islands (220 m), Stewart Island (0–300 m), South Island (0–1200 m), North Island (100–1310 m), Chatham Islands (80–240 m); Australia: Tasmania, Victoria, New South Wales. In New Zealand known from Fiordland, Southland, Otago, Canterbury, Westland, Western Nelson, Sounds–Nelson, Marlborough, Southern North Island, Taranaki, Volcanic Plateau, Gisborne, Auckland and Northland EPs.

A species that appears to occur under drier conditions than *Solenostoma orbiculatum*. The species is not a component of the stream-course bryoflora, while *S. orbiculatum* is common there. Also, it is more frequent than *S. orbiculatum* at upper elevations and occurs more often in the alpine zone, whereas *S. orbiculatum* is only exceptionally alpine. In the forest zone *S. inundatum* occurs on partly shaded, clayey, ± vertical, often bryophyte-covered banks within forests or at roadsides, and may be abundant under these conditions. It is found on such banks with *Achrophyllum quadrifidum*, *Breutelia elongata*, *Bryum blandum*, *Dicranella gracillima*, *Isotachis montana*, *Phaeoceros carolineanus*, *Pohlia wahlenbergii*, *Polytrichadelphus magellanicus*, *Telaranea tetrapila* and *Triandrophyllum subtrifidum*. At Mt. Arthur Hut Track (Kahurangi Natl. Park, 1050 m) on a vertical clay bank of a large sinkhole, ca. 3–4 m in diam. and ca. 2 m deep in a *Nothofagus menziesii* forest. In the alpine zone it was found in small boggy areas fed by small flushes, and here at the gravelly margin of a flush and among cushion plants within the flush (Symes Road, Old Man Ra., Otago, 1040–1570 m). Also over soil at the side of a rill in a mosaic of alpine tussock grass, rills and small rocky outcrops (Otira Valley Track, Arthur's Pass Natl. Park, 1210–1310 m).

Comments: *Solenostoma inundatum* has a characteristic aspect. The plants are typically erect, lax and soft-textured, and grow in compact tufts, often partially buried in the substrate. The color is usually a pale yellowish green to brownish green, or tinged with purplish red, and the leaf surface finely striolate to almost smooth. Both the perianth and subtending bracts appear disproportionately large for the plant size. The perianth is narrowly cylindrical in outline, and when dry is shaped like a Greek amphora: terete in the basal portion, then contracted to a deeply furrowed, ± twisted neck, and lacking a distinct beak.

Solenostoma orbiculatum (p. 703), when growing erect in dense tufts, may be confused with *S. inundatum*, but is usually a somewhat larger plant, with more obliquely inserted leaves and larger, laxer leaf cells; in *S. orbiculatum* the perianth is ± inflated, ellipsoid in outline and abruptly contracted to a distinct beak.

Solenostoma rufiflorum (Colenso) J.J.Engel

[Fig. 152: 3, oil-bodies, p. 698]

Jungermannia rufiflora Colenso, Trans. & Proc. New Zealand Inst. 18: 237. 1886. *Solenostoma rufiflorum* (Colenso) J.J.Engel, Novon 17: 312. 2007. Lectotype (*fide* Váňa, 1975): New Zealand, North Is., Waipawa Co., near Norsewood, 1885, *Colenso a. 1361* (WELT – *c. sporo.*); isolectotypes: (G! – *c. sporo.*, MPN, *non vidi*).

Plants delicate, thread-like, suberect to erect, in compact mats, ± nitid when dry, typically deep reddish brown to wine-red, minute, to 0.7 mm wide. Branching sparing to rather copious, the branches lateral-intercalary. Stem brownish green to wine-red, the cortical cells in surface view conspicuous, quadrate, thin-walled, smooth to finely papillose, in cross section the cortex moderately well differentiated, in 1(2) layers of deeply pigmented cells equal to or slightly larger than the medullary cells, their tangential walls often ± thickened; medullary cells pale, thin-walled. Rhizoids sparsely produced, almost absent from aerial portions of shoot. Leaves erect-appressed to obliquely spreading, distant, concave, shell-like, the insertion ± transverse, the leaves ovate to short-elliptic, entire, 360–575(640) μm wide × 385–560(630) μm long, the apex rounded; margins incurved, the dorsal margin decurrent as a narrow wing extending almost to the insertion of the next lower leaf, the ventral margin weakly decurrent. Cells firm-walled, trigones medium and straight-sided to bulging, the cells of lower median and basal portions of leaf short-rectangular, 17–20 μm wide × 24–27 μm long, the cells in distal sector smaller, 15–16 μm wide × 18–22 μm long; surface smooth to obscurely roughened (in older portions of plant) to coarsely papillose, not guttulate, the papillae on cells of distal sector of leaf low, 3.8–4.8 μm in diam., 10–15 per cell, the surface in basal cells closely striolate. Oil-bodies occupying a conspicuous portion of cell lumen, pale smokey grey, 3(4) per median leaf cell, very finely papillose, broad-elliptic to narrow-elliptic, most 4.8–7.2 × 10.6–12.5 μm, some 4.8 × 13.9 μm, less often globose and 5.8–6.7 μm in diam. Underleaves absent. Asexual reproduction absent.

Apparently dioecious. Androecia not seen. Gynoecia terminal, the shoots often innovating by numerous intercalary proliferations; bracts usually larger than the subgynoecial leaves, broadly ovate-elliptic, transversely inserted, not united with the perianth base. Perianth rather small, exceeding the bracts by half, ovoid-elliptic in outline, plicate in upper 0.5, tapering to an inconspicuous beak, the margins of the perianth mouth irregularly crenulate by bluntly

projecting ends of the marginal cells, the marginal cells not much elongated; cells of perianth proper similar to the leaf cells.

Capsule dark red, the wall 2-stratose, 26–30 μm thick, the outer layer ca. 1.7× the inner layer in thickness; outer layer of cells short-rectangular, thin-walled or with very thin continuous, sheet-like thickenings, with knob-like thickenings of both the longitudinal and transverse walls; inner layer of cells with longitudinal walls with thin, sheet-like, pigmented thickenings and regular, narrow, complete scalariform bands or the bands attenuated and ending short of the opposite wall.

Spores wine-red, 14.4–17.3 μm in diam., papillose, the papillae mostly sharply distinct or united into short rows of 2–3 papillae. Elaters 6.7–7.2 μm wide, bispiral, the ends tapering to a short, sinuous-twisted tip, the spirals 2.4–2.9 μm wide, extending to the elater tips.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands (600 m), South Island ([490]820–1480 m), North Island (1700–2025 m). Known from Fiordland, Southland, Otago, Westland, Western Nelson, Sounds–Nelson (Mt. Richmond) and Volcanic Plateau EPs.

A plant typically of exposed situations above ca. 500 m. Plants occurred on a ridge immediately north of Sewell Peak (820 m, Paparoa Ra., Westland) over pebbly soil of an exposed talus slope with some *Nothofagus solandri* var. *cliffortioides* and *Leptospermum scoparium*. In penalpine and alpine sites in exposed niches such as over soil of an exposed ridge with alpine vegetation at 1250–1450 m (below and W of Mt. Armstrong, Mt. Aspiring Natl. Park). At Rainbow Skifield (St. Arnaud Ra., Nelson Lakes Natl. Park) occurring on a slope at the edge of a tarn at 1360–1480 m in a mosaic of tussock grass and alpine vegetation along with tarns, rills, rocky outcrops and boulderfields. Also in an alpine fellfield on a flat area at a cliff base (1700 m, headwaters of Mangawhero River, Tongariro Natl. Park). Just south of the Top of the Bruce (N slope of Mt. Ruapehu, Tongariro Natl. Park) occurring over a thick soil layer in a rock crevice at 2025 m in an area of cliffs and outcrops with scattered alpine plants. The species has been found with *Austrolophozia paradoxa*, *Bartramia papillata*, *Conostomum pentastichum*, *Dicranoweisia antarctica*, *Dicranum aucklandicum*, *Diplophyllum domesticum*, *Ditrichum difficile*, *D. punctulatum*, *Hygrolembidium acrocladum*, *Isotachis intortifolia*, *Kurzia hippuroides* and *Rhacocarpus purpurascens*.

Comments: Among the distinctive features of this species is the conspicuous, turgid, quadrate cortical cells, which have deeply pigmented walls, and a characteristic transparent appearance, almost resembling a hyaloderm. This species and *Solenostoma totipapillosum* are the smallest members of the genus present in New Zealand, but *S. rufiflorum* is typically the smaller of the two. They are likely to be confused because the leaves of both are distinctly papillose. The distal leaf cells of both species are about equal in size, but the individual papillae of *S. rufiflorum* are smaller than those of *S. totipapillosum*, and there are consequently more papillae per cell (8–15 per cell, Fig. 152: 3 vs. 3–5 per cell in *S. totipapillosum*, Fig. 152: 4). In the basal portion of the leaf the surface is closely striolate, with welt-like papillae. The papillae are best seen on young leaves, since in older portions of the plant the papillae often become eroded and indistinct. The spores of *S. rufiflorum* may also be larger than those of *S. totipapillosum*: 14.4–17.3 μm vs. 12.5–13.4 μm in diam. For other differences, see the discussion under the latter species (p. 711).

Solenostoma totipapillosum (E.A.Hodgs.) R.M.Schust.

[Plate 13A; Fig. 152: 4, oil-bodies, p. 698]

Jungermannia totipapillosa E.A.Hodgs., J. Roy. Soc. New Zealand 2: 111. 1972 ("*totopapillosa*"). *Solenostoma totipapillosum* (E.A.Hodgs.) R.M.Schust., Beih. Nova Hedwigia 119: 379. 2002 ("*totopapillosum*"). Holotype: New Zealand, South Is., Governors Bush, Mt. Cook, 19 Sept. 1962, *J. Taylor* (MPN 19433 ex herb. Hodgson 12983, *non vidi*); isotype: (CHR 1135674!).

Plants delicate, thread-like, prostrate to ± erect, in loose mats, dull, pure green to light green to yellowish green tinged with red, to deep wine-red, minute, to 1 mm wide. Branching sparing to rather copious, the branches lateral-intercalary. Stem green to dark- to brownish green to wine-red, the cortical cells in surface view narrowly rectangular, the cell outlines obscure, the walls often rather thick, often coarsely papillose like the cells of the leaves, in cross section the cortex not sharply differentiated, in a single layer of somewhat smaller cells; medullary cells large, thin-walled. Rhizoids sparsely produced, almost colorless, diffusely arranged, from the ventral side of the stem. Leaves often subvertical, obliquely to widely spreading, distant, moderately concave, the insertion weakly succubous to ± transverse, the leaves oval to broadly elliptic to almost orbicular, 490–590(750) μm wide × 390–490 μm long, the apex broadly rounded; margins plane to ± erect, the dorsal and ventral margins only weakly decurrent. Cells opaque, firm-walled, trigones small to medium and straight-sided; cells of lower median and basal portions of leaf short-rectangular, to 18–21(35) μm long, the cells in distal sector smaller, ± isodiametric, 13–20 μm wide and long; surface coarsely papillose, with large oval papillae, the papillae 3–5 × 6–8 μm, 3–5 per cell in distal portion of leaf. Oil-bodies pale smokey grey, dull opaque, 2–4(5) per median leaf cell, coarsely granular, short to rather long-elliptic, at times somewhat irregularly so, 4.8–6 × 8.6–13 μm. Chloroplasts large for the cell size. Underleaves absent. Asexual reproduction absent.

Dioecious. Androecial shoots a little narrower than ♀ ones, the androecia intercalary, with bracts in 3–6 pairs, strongly ventricose, rather distant, transversely inserted, the bract margins broadly recurved; antheridia solitary, rarely 2 per bract, the stalk biseriate. Gynoecia terminal, the shoots often innovating by one or more stout intercalary branches; bracts almost the same size as the subgynoecial leaves, broadly elliptic to ovate or cordate, transversely inserted, not united with the perianth base or with 1 bract inserted on it. Perianth exceeding the bracts by half, turbinate (obpyriform), terete below, bluntly 4–5-angled in the distal 0.3–0.5 and abruptly narrowed to an erect, collar-like, prominent beak, the margins of the perianth mouth crenulate by bluntly projecting ends of the marginal cells, the cells of the beak subquadrate to short-rectangular (to 2.5:1); cells of perianth proper similar to the leaf cells, isodiametric, coarsely papillose.

Capsule dark red (the valves carmine by transmitted light), short-ellipsoidal to subglobose, the wall 2-stratose, 30–32 μm thick, the outer layer about 2× the inner layer in thickness; outer layer of cells short-rectangular, thin-walled or with very thin continuous, sheet-like thickenings, with short peg-like to knob-like thickenings of both the longitudinal and transverse walls, often extending a short distance onto the outer tangential wall; inner layer of cells with longitudinal walls with thin, sheet-like, pigmented thickenings and regular, narrow, complete scalariform bands, only rarely ending short of the opposite wall.

Spores 12.5–13.4 μm in diam., carmine, papillose, the papillae mostly distinct or united into short ridges of 2–4 papillae. Elaters 7.7–8.6 μm wide, bispiral, the ends abruptly taper-

ing to elongate, sinuous-twisted tips, the tip portion 3.4–3.8 μm wide, the spirals 3.4–3.8 μm wide, not extending into the elater tips.

Distribution and Ecology: Endemic to New Zealand: South Island ([450]760–1970 m), North Island (1200–1350 m). Known from Fiordland, Southland (Garvie Mtns.), Otago (Central Otago), Westland, Canterbury, Western Nelson, Sounds–Nelson and Volcanic Plateau EPs.

A plant of well-drained, often exposed sites. In forests above 450 m over dripping cliff faces or clayey soil of slopes or banks. At 450 m in lower montane *Nothofagus fusca* forest with *Dacrydium cupressinum*, *Metrosideros umbellata* and *Griselinia littoralis* where it is on clayey soil of a slope (Paparoa Ra., along Croesus Track, Westland). Plants at the type locality (Governors Bush, Mt. Cook Natl. Park, 760–800 m) formed a soft, velvety, loose mat over a shaded cliff face in a *N. menziesii* forest. Also in upper montane forests of *N. fusca – N. solandri* var. *cliffortioides* (e.g., on a clayey bank at Pinchgut Track, Nelson Lakes Natl. Park, 1280–1390 m). In penalpine areas of *Chionochloa*, *Hebe* and *Dracophyllum* occurring over pebbly soil of a steep slope at 1010–1170 m just southwest of Mt. Burns (Fiordland Natl. Park) or deep in a pocket in the side of a rill at 1370–1470 m below and west of Mt. Shrimpton (Mt. Aspiring Natl. Park). On the track to the summit of Mt. Arthur (Kahurangi Natl. Park) occurring at 1550 m on soil in a protected pocket halfway down a large sinkhole (ca. 3–4 m in diam. × 3–4 m deep); the immediate habitat included mosaic communities of penalpine cushion vegetation, rocky herbfields and *Dracophyllum*. In the alpine zone at the lip of a seepage area (head of Gertrude Valley, Fiordland Natl. Park, 1940–1970 m) or on a cliff face where some soil has accumulated (Stocking Stream, Mt. Cook Natl. Park, 1280–1330 m). In the North Island found deep in a crevice between boulders at ca. 1200 m in an area with alpine vegetation with scattered frequent rocky outcrops (Mangatepopo Stream below Soda Springs, Tongariro Natl. Park, Wellington). The species has been found with *Conostomum pusillum*, *Diplophyllum dioicum* var. *icari*, *D. domesticum*, *Ditrichum difficile*, *Hygrolembidium australe*, *Jensenia connivens*, *Kurzia hippuroides*, *Leptotheca gaudichaudii*, *Marsupella ustulata* and *Notoligotrichum australe*.

Nomenclature: Váňa (1975) selected a specimen from CHR as lectotype of *Jungermannia totipapillosa*. However, Hodgson did not have direct involvement with the identity of the CHR specimen, as the collection has only a typed Botany Division paper determination slip that states "135647 Clasmatocolea sp. nov. Determinavit E.A.Hodgson 1964," and a typed supplementary label stating "Clasmatocolea sp. nov. papillose: assoc. Diplophyllum obtusum, E.A.Hodgson 1964." The specimen bears no handwriting of Hodgson. A specimen at MPN, on the other hand, bears the notation, "Jungermannia spec. nov." and, beneath, "= Jung. totopapillosa Hodgs.," with "Type" written in red ink on the packet, all in Hodgson's hand. We conclude that the MPN specimen is the holotype, and the CHR collection an isotype.

Comments: *Solenostoma totipapillosum* is a distinctive plant, despite its diminutive size. The plants are typically a dull, light green, with distant, widely spreading, transversely inserted leaves. The most distinctive feature of the plant is the high, spherical papillae (Fig. 152: 4), which viewed from the side (or in sections of the leaf) resemble droplets of oil or resin, hence the term "guttulate" used to describe papillae of this type. Other notable features of *S. totipapillosum* are the rich carmine color of the spores and the oddly shaped perianth, with its erect beak, which resembles an old-fashioned stand-up collar. *Solenostoma totipapillosum* is commonly found under forest, whereas the very similar *S. rufiflorum* has not been recorded from forest habitats.

According to Váňa (1975), *Solenostoma totipapillosum* is the only non-Asiatic species of

the sect. *Nematocaulon*, the members of which are characterized by the coarsely papillose surface of the leaves. It may be confused with *S. rufiflorum*, but in this species the papillae are low, smaller in diameter and 8–15 per cell.

Uncertain Species

Solenostoma novaezelandiae R.M.Schust., Beih. Nova Hedwigia 119: 380. *f. 354: 1–3*. 2002. Type: New Zealand, South Is., S of Haast, *Schuster FAA–1041*.

We are uncertain of the status of the species, and we have not examined the type. The leaf size (1.5 × 1.6–3.2 mm) and the bistratose capsule wall fit our concept of *Solenostoma orbiculatum*, where this species seems to belong.

Subfam. ***Jamesonielloideae*** Inoue

Subfamily *Jamesonielloideae* Inoue, J. Hattori Bot. Lab. 29: 178. 1966.

Jamesoniella (Spruce) Carrington *in* Lees

Jamesoniella (Spruce) Carrington *in* Lees, London Cat. Brit. Moss Hepat., ed 2. 25. 1881. *Jungermannia* subg. *Jamesoniella* Spruce, J. Bot. 14: 202, 230. 1876.

Plants opaque, usually erect, exceptionally procumbent, yellow-green to, commonly, orange-brown to brownish red to deep carmine to fuscous, typically dull and not nitid, medium to vigorous, to 3 mm wide, the shoot tips inclined upward. Branching sparing, with terminal branches, when present, always of *Frullania* type; ventral-intercalary branches present; stoloniform, microphyllous branches usually absent. Stems with cortical cells strongly differentiated, with thickened walls and strong corner thickenings; paraphyllia lacking on sterile shoots. Rhizoids colorless, in most species also at shoot tips, often abundant, scattered, rarely mostly at ventral base of leaves. Leaves with orientation variable, ± vertical and erect to subhorizontal and widely spreading, imbricate, subtransversely to succubously oriented, the insertion obliquely succubous in dorsal half, extending to stem midline dorsally but not beyond, the ventral sector basiscopic, often ± strongly recurved, not or shortly decurrent, the dorsal margin scarcely short- to long-decurrent, the leaves undivided, entire, the ventral bases not strongly ampliate. Cells ± rounded-hexagonal, the median cells ± thin-walled, with trigones concave- to convex-sided, at times strongly bulging and knot-like, the trigones rarely lacking; surface often smooth or conspicuously papillose in median sector of leaf, the base finely striate to coarsely papillose. Oil-bodies 5–20 per cell, finely granular to papillose to botryoidal. Underleaves minute and ephemeral, in some species ± distinct, lanceolate; ventral merophytes ± narrow. Asexual reproduction absent (leaves somewhat fragile and fragmenting in *Jamesoniella rubricaulis*).

Dioecious (abnormally paroecious; cf. Grolle, 1971a, p. 34). Androecia terminal but becoming intercalary, ± spicate, the bracts in 4–10 pairs, mostly smaller than vegetative leaves, strongly ventricose, the dorsal base with an inflexed lobule, the lobule margin at times with a tooth; antheridia 1 per bract (2–3 in *Jamesoniella undulifolia*), the stalk 2-seriate ([2]4-seriate in *J. undulifolia*); paraphyllia often present between the bracts. Gynoecia with subinvolucral

bracts strongly differentiated from leaves, the innermost series smaller than outer 1–2 series, often dimorphic, variously and irregularly armed, lobulate/laciniate and/or armed with cilia or teeth; bracteole large, nearly as long as bracts, usually over 0.25 area of bracts, elongate to lanceolate, variously armed or lobed, at least on flanks. Perianth at least 0.5 exserted, cylindrical-ovate, terete toward base, distally ± deeply 4–5-plicate (toward mouth sometimes secondarily to 10-plicate), the plicae straight and not twisted, rarely eplicate; perianth 2–several-stratose toward base.

Seta with numerous, ± equal-sized cells. Capsule ovoid-ellipsoidal, the wall 4–5(8)-stratose; outer layer of cells higher than any internal strata, with strong I-shaped, nodular thickenings; innermost layer of cells with semiannular bands.

Spores 14–30 μm in diam., granular to finely papillose, short-vermiculate to verrucate (coarsely and irregularly warty) or densely and strongly baculate. Elaters at times adhering to valve surface long after capsule dehiscence, (1)2(3)-spiral, 7–12 μm wide.

Type: *Jamesoniella colorata* (Lehm.) Schiffn. (≡ *Jungermannia colorata* Lehm.)

A genus of, currently, 14 species. Grolle divided the genus into five sections, of which three occur in Austral areas:

1) sect. *Robustae* Grolle, with *J. kirkii*;

2) sect. *Jamesoniella* (type = *J. purpurascens* Steph.; cf. Grolle, 1971a, p. 55), including *J. tasmanica*, with a rather broad distribution in temperate Australasia, and *J. purpurascens* of South Africa (Cape), Transvaal, northeastern Madagascar, Mascarenes (Réunion, Mauritius) (Grolle, 1971a, p. 62);

3) sect. *Coloratae* Grolle, including *J. colorata*, with a pan-south-temperate distribution; this is the only representative of the genus in southern South America.

Note that Schuster (2002a, p. 405) mentioned sect. *Purpurascentes* R.M.Schust. in a key, but the name is not found elsewhere; Schuster included *Jamesoniella tasmanica* and *J. purpurascens* in the section.

Kitagawa (1981) treated *Cuspidatula* as a synonym of *Jamesoniella*; they are treated as discrete genera here. In *Jamesoniella* the leaves are rounded at the summit and the ♀ bracts are never deeply 2–3-fid vs. leaves strongly tapered and sharp and ♀ bracts deeply 2(3)-fid to 0.45–0.6 in *Cuspidatula*.

References: Grolle (1971a); Schuster (2002a).

Key to Species

1a. Plants plagiochiloid, with leaves spreading, the distal portion broadly reflexed, horizontally oriented, distinctly convex; underleaves conspicuous, laminar, subulate to narrowly elliptic, rarely deeply bifid . . . . . *J. tasmanica* (p. 719)

1b. Plants not plagiochiloid, the leaves ± dorsally assurgent, vertically oriented, distinctly concave; underleaves inconspicuous, spine-like or filamentous 2

2a. Leaves orbicular to broadly elliptic, shell-like, the margins narrowly inflexed throughout, otherwise plane and not undulate; leaf cells with trigones small to medium and straight-sided; plants terricolous or saxicolous . . . . . *J. colorata* (p. 722)

2b. Leaves elliptic to oblong-ovate, channeled, the dorsal margins transversely undulate; leaf cells with trigones knot-like and confluent; plants corticolous . . . . . *J. kirkii* (p. 717)

Since plants of *Jamesoniella* may be confused with those of *Cryptochila* we have provided a separate, artificial key that combines the species of these two genera. (See also the key to distinguish *J. colorata* and *Cryptochila grandiflora* on p. 740.)

Artificial Key to Species of *Jamesoniella* and *Cryptochila* based upon Vegetative Characteristics

1a. Leaves lingulate, tightly shingled and appressed to stem in ventral aspect (shoots plano-convex), the dorsal margins stiffly vertically oriented 2
- 2a. Dorsal leaf margins regularly transversely undulate, unistratose throughout; median leaf cells with coarsely knot-like and in part confluent trigones; corticolous. Rather common, South and North Is. . . . . *Jamesoniella kirkii* (p. 717)
- 2b. Dorsal leaf margins not undulate, the decurrent base thickened, 2–3(4)-stratose; median leaf cells uniformly thick-walled, without trigones; terricolous. Rare, Campbell Is., Stewart Is., western South Is. . . . *Cryptochila acinacifolia* (p. 742)

1b. Leaves elliptic-ovate, orbicular to subreniform, not lingulate, not ventrally shingled and appressed to stem 3
- 3a. Dorsal leaf bases strongly interlocking dorsally, not or weakly decurrent dorsally. Cells with walls thin, trigones distinct, medium to knot-like; surface of median and distal leaf cells smooth . . . . . *Cryptochila nigrescens* (p. 734)

3b. Dorsal leaf bases not interlocking, the dorsal margins distinctly decurrent 4
- 4a. Leaves coarsely papillose, the papillae large, crowded, guttulate. Plants often tinted with red or reddish throughout . . . . . *Jamesoniella colorata* (p. 722)
- 4b. Leaves smooth, or striate-papillose only in basal portion 5
  - 5a. Plants lax, the leaves horizontally spreading, ovate to elliptic-ovate; underleaves often present and subulate, united to at least one leaf at ventral base . . . . . *Jamesoniella tasmanica* (p. 719)
  - 5b. Plants ± rigid, the leaves strongly ventrally secund, ± appressed to stem (particularly when dry), orbicular to reniform; underleaves absent or reduced to a uniseriate filament 6
    - 6a. Leaves usually distinctly squarrose when moist, the dorsal leaf margin erect-inflexed to involute. Plants often greenish, at times deep reddish brown to deep wine-red; cells moderately to strongly and evenly thick-walled, trigones lacking or very small and indistinct . . . . . *Cryptochila grandiflora* (p. 736)
    - 6b. Leaves rigidly convex, not squarrose, the dorsal leaf margin tightly and narrowly revolute from base to apex . . . . . *Cryptochila pseudocclusa* (p. 740)

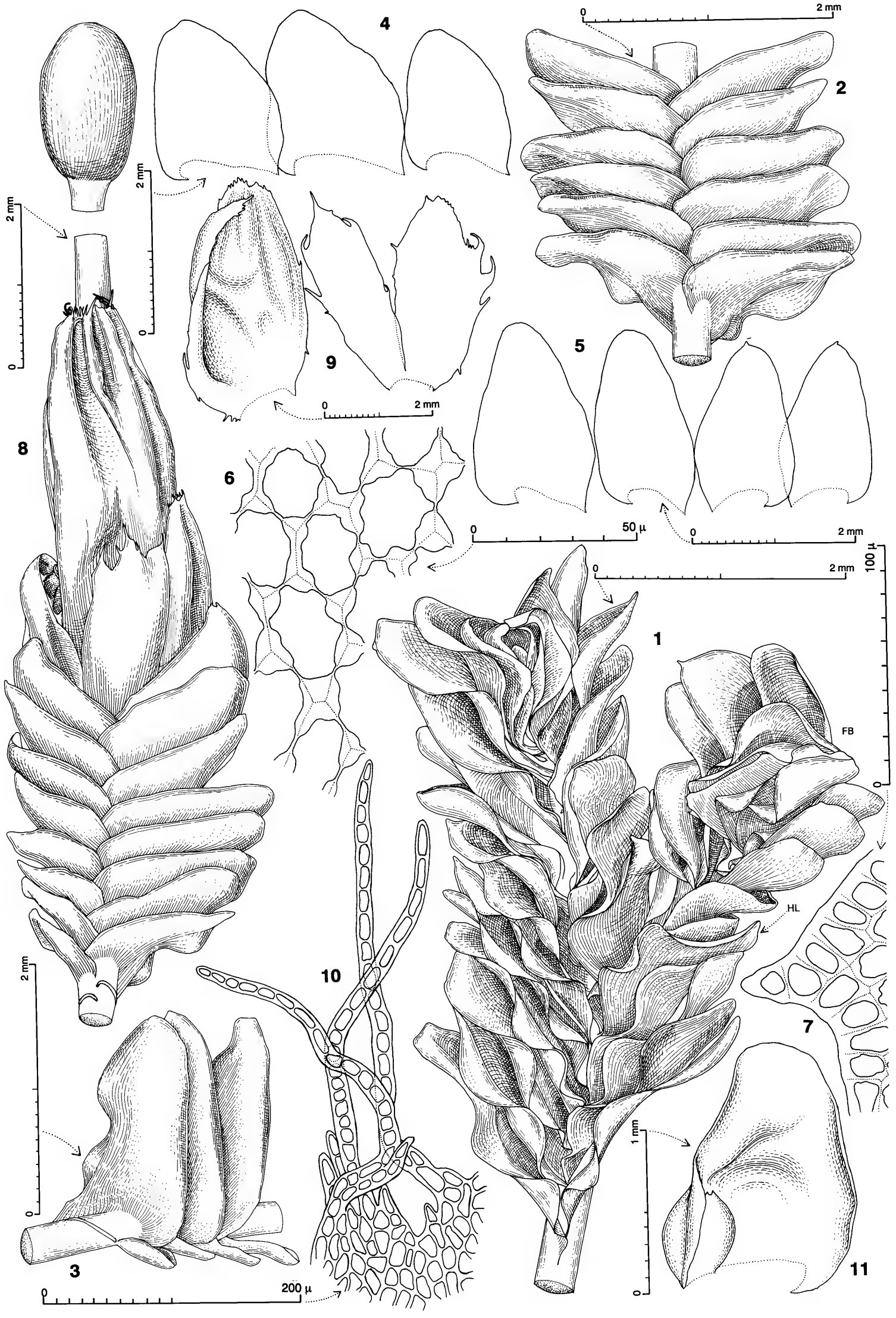

Fig. 155.
Jamesoniella kirkii Steph. 1. Portion of shoot with *Frullania*-type branch (= FB; HL = half-leaf), dorsal view. 2. Portion of shoot, ventral view. 3. Portion of shoot, lateral view. 4, 5. Leaves. 6.

Jamesoniella kirkii Steph.

[Plate 14A; Fig. 155; Fig. 158: 1, oil-bodies, p. 724]

Jamesoniella kirkii Steph., Hedwigia 34: 47. 1895. Type: New Zealand, North Is., Bay of Islands, *Kirk 75* (*fide* Grolle, 1971a).

Jamesoniella scolopendrina Berggr., New Zealand Hepat. 16. *f. 12*. 1898. Lectotype (*fide* Grolle, 1971a): New Zealand, South Is., Bealey River, 600 m, *Berggren 2840* (LD, *non vidi*).

Jamesoniella allisonii E.A.Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 81. 1965. Holotype: New Zealand, South Is., Central Otago, above Queenstown, ca. 1200 ft., *Allison H6301* (herb. Hodgson no. 11592) (MPN, *non vidi*); isotype: (CHR ex herb. Allison!).

Plants procumbent, adhering to substrate, the shoot tips slightly ascending, light green to yellow-brown, occasionally reddish tinged, occasionally red throughout in exposed sites, to 5 cm long, to 4 mm wide. Stems becoming brownish, the cortex poorly differentiated, the cortical cells slightly smaller, with ± evenly thickened walls, often ± yellowish brown; medullary cells with ± strongly and unevenly thickened walls. Rhizoids from ventral side of stem, extending almost to shoot apex. Branching rather frequent, pseudo-dichotomous, of terminal, *Frullania* type, occasionally ventral-intercalary; stolons rarely present, with shell-like leaves. Leaves distinctly dorsally assurgent (stiffly and more strongly so when dry), in ventral view the shoots strongly convex, the leaves in ventral aspect appearing precisely shingled in a smooth plane (plano-distichous), their ventral margins parallel and aligned nearly at right angles to the axis, the dorsal margins vertically oriented (seen on edge in dorsal view) and distinctly and quite regularly undulate, the leaf insertion ± longitudinal, then very obliquely succubous, not recurved at ventral end; leaves typically short-elliptic, less often oblong-ovate or broadly ovate, 1500–1900 μm wide, 1700–1950 μm long, entire, subcanaliculate, sometimes subcucullate toward the apex, the ventral margin narrowly inflexed; apex broadly rounded to subacute, at times apiculate; dorsal margin broadly arched to ± straight distally and broadened and weakly ampliate below, short-decurrent; ventral margin weakly arched, abruptly contracted at extreme base, the ventral leaf bases overlapping but not completely hiding the stem. Cells not porose, with thin walls, the trigones coarsely knot-like and in part confluent; cells of upper median portion of leaf hexagonal, 19–22 μm wide × 20–30 μm long; cells toward the median-leaf base gradually somewhat broadened and more strongly elongated, with knot-like trigones; leaves with an indistinct border formed by 1–2 rows of somewhat smaller and more evenly thick-walled cells; surface smooth, the basal leaf cells finely papillose. Oil-bodies smokey grey, 5–8(10) cell in per cell in median-upper sector of leaf, 8–10 per cell at leaf base, 3–5 per cell at leaf margin, moderately botryoidal, globose and 5.5–7 μm in diam. or elliptic and 4.5–7 × 13–16 μm, some 8 × 9 μm. Underleaves inconspicuous, present toward shoot apices, caducous below, irregularly filamentous.

Androecia on main shoot or *Frullania*-type branches, narrower than vegetative portions of shoot, with 2–5 pairs of bracts; bracts strongly saccate in basal portion, winged, the dorsal

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Upper median leaf cells. 7. Apiculate leaf apex. 8. Gynoecium with mature sporophyte, ventral view. 9. Innermost ♀ bracts and, in middle, bracteole (adaxial view). 10. Portion of perianth mouth. 11. ♂ Bract (note wing). (Figs. 1–3, 5–10, from *Engel 18000*, New Zealand, South Is., Westland EP, Mt. Aspiring Natl. Park, summit area of Haast Pass; 4, from *Engel 19123*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., N side of Fox R.; 11, from *Reif C126A*, New Zealand, South Is., Westland EP, Alexander Ra., Camp Creek.)

margin of the bract often decurrent as a narrow abaxial wing (the lobule thus seemingly inserted on the adaxial face of the bract); lobule large, broadly inflexed, the apex acuminate, the free margin entire or with a tooth; antheridia single, the stalk biseriate. Gynoecia mostly innovating; bracts strongly differentiated from leaves, gradually increasing in size toward perianth, those of innermost series the largest, free from one another, deeply concave to cochleariform, often longitudinally plicate, retuse to bifid, the lobe tips sharply apiculate, the bract margins entire or with a few slender or broad-based teeth; bracteole narrowly elliptic, free or united with one of the bracts, nearly as long as the bracts, the apex ending in a sharp apiculus, the margins with a few slender, sharp teeth. Perianth narrowly elliptic-obovate, deeply plicate in the upper 0.65–0.75, strongly contracted to the mouth, the mouth margin lobulate, the lobules densely armed with long, ciliate hairs, the hairs uniseriate, to 20 cells long, the cells not elongate; cells of lobules with evenly thickened walls, those of the perianth proper with well-developed trigones like the leaf cells.

Capsule intensely reddish pigmented, ellipsoidal, the wall 78–85 μm thick, 5–6-stratose; outer layer of cells with radial longitudinal walls with strong, nodular thickenings, the thickenings of adjoining cells frequently in opposing pairs, the transverse walls rarely with an isolated nodular thickening; innermost layer of cells with semiannular bands common, close, wide, nearly always complete, sometimes forked and delimiting local fenestrae.

Spores 15–20 μm in diam., verruculose. Elaters bispiral, 7–8.2 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (near sea level to 1000 [1200] m), North Island (40–1300 m). Known from Fiordland, Southland, Otago, Westland, Canterbury, Western Nelson, Marlborough, Sounds–Nelson, Southern North Island, Volcanic Plateau, Gisborne and Auckland EPs.

A forest species that is nearly exclusively corticolous, and is recorded from the trunks of *Nothofagus menziesii*, *N. truncata*, *Archeria traversii* and *Weinmannia racemosa*. It is found in upper montane forest, particularly on ridges exposed to drying winds, of *N. menziesii*, *N. fusca*, *W. racemosa* and *Dracophyllum traversii – A. traversii* forests. It is frequently associated with *Cuspidatula monodon*, at times forming thick, loose mats, at times occurring as scattered, small patches. It may tolerate considerable exposure, present, for example, on bark of small trees that occur with a few scattered shrubs and grasses on otherwise exposed bare rock on the slopes of the Franz Josef Glacier Valley (off Roberts Point Track, SW of Mt. Gunn, Westland Natl. Park, ca. 510–570 m). It rarely has been collected from rock or from rotten logs. Species found with *Jamesoniella kirkii* are *Bunodophoron scrobiculatum*, *Calyptopogon mnioides*, *Frullania aterrima*, *Goebeliella cornigera*, *Herbertus oldfieldianus*, *Hypnum chrysogaster*, *Leifidium tenerum*, *Lepicolea scolopendra*, *Lepidolaena reticulata*, *Leptotheca gaudichaudii*, *Lepyrodon lagurus*, *Macromitrium longipes*, *Paraschistochila tuloides*, *Pseudomarsupidium piliferum* and *Wijkia extenuata*.

Comments: The stiffly upswept leaves (Fig. 155: 3) with distinctly undulate dorsal margins (Fig. 155: 1) and pseudo-dichotomous branching (Fig. 155: 1) make this one of the most unmistakable of New Zealand hepatics. The ventral aspect of the plant also is unusual for the genus in the widely divergent, strictly parallel and tightly appressed arrangement of the leaves (Fig. 155: 2). The leaves are tongue-like, with apices either broadly rounded or minutely apiculate, and the leaf cells have strongly developed, knot-like, often confluent trigones (Fig. 155: 6; Fig. 158: 1).

The relatively rare *Cryptochila acinacifolia* also has lingulate leaves (Fig. 163: 4) but with non-wavy dorsal margins (Fig. 163: 3) that are 2–3-stratose near the base (Fig. 163: 6), the leaf cells uniformly thick-walled, lacking trigones (Fig. 163: 7), and it is never epiphytic.

Jamesoniella tasmanica (Hook.f. & Taylor) Steph.

[Plate 14F; Fig. 156; Fig. 158: 2, oil-bodies, p. 724]

Jungermannia tasmanica Hook.f. & Taylor *in* Taylor, London J. Bot. 5: 274. 1846. *Mesophylla tasmanica* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 398. 1877. *Jamesoniella tasmanica* (Hook.f. & Taylor) Steph., Sp. Hepat. 2: 100. 1901. Type: Tasmania, *Gunn*.

Jamesoniella cambewarrana Steph., Sp. Hepat. 6: 97. 1917. Type: Australia, Cambewarra, *Watts*; New Zealand, Great Barrier Is., *Hooker* (cf. Grolle, 1971a).

Plants distinctly plagiochiloid in aspect, procumbent and firmly adhering to the substrate, the shoot tips very weakly ascending, the plants green or tinged with claret red, at times ± intensely red, to 4 mm wide. Stems thick, fleshy, colorless or rarely weakly reddish, the cortical cells in 1–2 layers, somewhat smaller, their walls somewhat more strongly thickened; medullary cells colorless, thin-walled. Rhizoids from ventral side of stem, extending almost to shoot apex. Branching infrequent, of terminal, *Frullania* type; half-leaf ovate, longitudinally inserted; first branch underleaf narrowly elliptic, at base of branch, entire or bifid (at times asymmetrically) almost to base; leading, leafy ventral-intercalary branches present; stolons lacking. Leaves horizontally spreading (at least distally) to strongly dorsally elevated, distinctly convex (in dorsal aspect), the margins ± broadly reflexed, the median basal portion of the leaf typically concave, somewhat hollowed out and laxly sheathing, the insertion steeply oblique in dorsal portion, becoming subtransverse, abruptly short-recurved at ventral end, the attachment equal to 0.65–0.75 the leaf width; leaves (when flattened) ovate to elliptic-ovate, 1250–2000 μm wide × 1600–1800 μm long, entire; apex rounded to weakly truncate, at times retuse to shallowly bifid; dorsal margin usually short-decurrent; ventral margin moderately decurrent (at times more so on one side of the shoot). Cells evenly thick-walled, but in median optical section appearing thin-walled and with small to medium and straight-sided trigones; cells of upper median portion of leaf 20–30 × 25–35 μm; cells toward the median-leaf base gradually enlarged; surface smooth or closely and finely striate, especially at base of leaf. Oil-bodies occupying a large proportion of the cell, hyaline and glistening, 16–20 per median leaf cell, moderately papillose, the spherules slightly protruding beyond the membrane, the oil-bodies irregular in shape: subglobose to broadly ovoid to broadly elliptic, a few sublinear, 4.8–5.3 × 5.3–6.2 μm to 3.8–4.8 × 7.2–8.2 μm, some 3.4 × 6.7 μm, sporadic ones large and 4.3–4.8 × 9.6–10.6 μm. Underleaves highly variable, minute, subulate, or at times larger and narrowly elliptic, rarely deeply bifid, usually united on one side with a leaf, on the opposite side decurrent or sometimes fused with the leaf opposite by a transverse ridge, the ridge with a minute apiculus representing the underleaf.

Androecia on leading shoots, not much narrower than vegetative sectors, with up to 12 pairs of bracts; bracts strongly saccate in basal portion, the dorsal margin of the bract decurrent as a broad abaxial wing (the lobule thus seemingly inserted on the adaxial face of the bract); lobule broadly lanceolate, the apex apiculate to acuminate, the free margin with 1–2 small teeth; antheridia solitary, the stalk biseriate. Gynoecia mostly innovating, notable when young and without a distinct perianth as a laciniate bud; bracts increasing in size toward perianth, those of innermost series markedly smaller, free from one another, one or both bracts of innermost series strongly laciniate-lobulate (fundamentally bilobed, with several accessory lobules and teeth); bracteole free, nearly equal to bracts in length, basically bilobed, at times with several accessory lobes, the margins with 1 or more teeth. Perianth elliptic to obovate, strongly plicate in the upper 0.25–0.35, strongly contracted to the truncate mouth, the mouth shallowly lobulate,

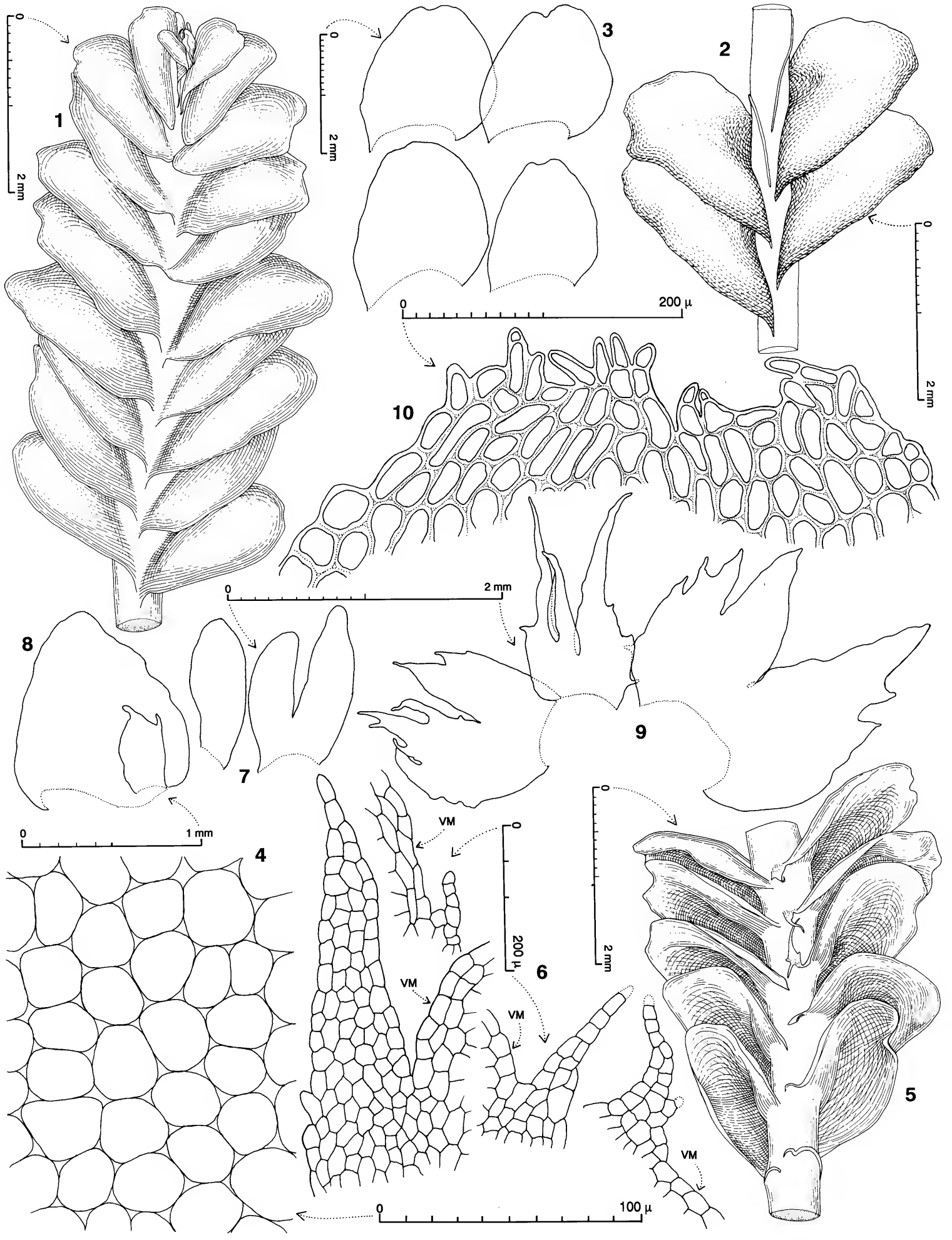

Fig. 156.
Jamesoniella tasmanica (Hook.f. & Taylor) Steph. 1. Portion of shoot, dorsal view. 2. Portion of shoot, dorsal view. 3. Leaf outlines. 4. Upper-median leaf cells. 5. Portion of shoot, ventral view. 6. Underleaves (VM = ventral margin). 7. Unlobed and lobed first branch underleaves. 8. Winged ♂ bract. 9. Innermost ♀ bracts and, in middle, bracteole. 10. Perianth mouth. (Figs. 1, 4, 5, 7, from *Engel 18762*, New Zealand, South Is., Fiordland EP, off track along East Branch of Eglinton R., SE of Mt. Eglinton; 2, from *Engel 20702*, New Zealand, North Is., Volcanic Plateau EP, Whirinaki Forest Park, near Whirinaki R., SSW of Minginui; 3, from *Engel 17978*, New Zealand, South Is.,

finely and irregularly denticulate by wholly or partially excurrent elongated cells; cells of lobules elongated, the cells below subisodiametric; perianth 2-stratose in basal 0.5.

Capsule ellipsoidal, the wall 5–6-stratose; outer layer of cells with the radial longitudinal walls with nodular thickenings, the transverse walls rarely with isolated nodular thickenings; innermost layer of cells with thickened longitudinal walls, with semiannular bands common, rather narrow, complete or tapering to a sharp point before reaching the opposite wall, sometimes forked but not anastomosing.

Spores 18–19 μm in diam., with fine papillae and short-vermiculate ridges. Elaters bispiral, 8–11 μm wide.

Distribution and Ecology: New Zealand: Auckland Islands (30 m), Stewart Island, South Island (50–720 m), North Island (100–760 m); Australia: Tasmania, Victoria, South Australia, New South Wales. In New Zealand known from Fiordland, Otago (Mt. Cargill, Lakes region), Canterbury (Mt. Cook Natl. Park), Westland, Western Nelson, Sounds–Nelson, Taranaki, Volcanic Plateau, Gisborne and Northland EPs.

The species is for the most part a lowland forest plant of *Nothofagus fusca*, *N. menziesii*, *N. solandri*, *Knightia excelsa*, *Weinmannia racemosa* and *N. truncata* forests, and typically occurs below 600 m. The species is not a pioneer, but rather grows in bryophyte-rich associations. It occurs on the forest floor, on bryophyte-covered banks, and, rather commonly, on old, rotted, bryophyte-covered, decorticated logs and at the bases of tree trunks and stumps. The species occasionally grows in open boggy areas with, for example, *Coprosma* spp., *Juncus squarrosus*, *Leptospermum scoparium* and *Ozothamnus leptophyllus* (Saddle W of road to Mt. Cargill, N of Dunedin, 500 m), and in Westland it has been found on soil in pakihi. It exceptionally occurs on rock, e.g., at the summit area of Haast Pass (510–560 m, Mt. Aspiring Natl. Park) it formed pure, thick, cushion-like masses over the side of a boulder. It occurs with *Bazzania adnexa*, *Chiloscyphus mittenianus*, *Cuspidatula monodon*, *Heteroscyphus cymbaliferus*, *Hymenophyton flabellatum*, *Hypnum chrysogaster*, *Lepidozia pendulina*, *Leptophyllopsis laxus*, *Leucobryum candidum*, *Pyrrhobryum bifarium* and *Rhizogonium pennatum*.

Comments: *Jamesoniella tasmanica* is distinctly *Plagiochila*-like in aspect (in particular, *P. banksiana*): the plants are soft-textured, with distinctly convex, horizontally spreading ovate to elliptic-ovate leaves, with broadly reflexed margins and a hollowed-out median basal portion (Fig. 156: 1–3).

The underleaves of *Jamesoniella tasmanica* are the best developed of any regional species of the genus, but there is considerable variation in underleaf form, even along the length of a single shoot. At one extreme, the underleaves are narrowly elliptic (rarely deeply bifid, and still more rarely free), but in the main the underleaves are represented by a small triangular to subulate process, basally united with the ventral margin of an adjacent leaf (Fig. 156: 5). In the absence of evident underleaves, there is often a low, arched ridge united to at least one (Fig. 156: 5, lower), and rarely both leaves, with the underleaf represented only a minute sharp tooth on the ridge.

The androecia of *Jamesoniella tasmanica* are notable for the strongly winged bracts, the lobules seemingly inserted on the adaxial face of the bract (Fig. 156: 8). The apex of the lobule is sharply acuminate and usually conspicuous even under the dissecting microscope.

Westland EP, Mt. Aspiring Natl. Park, summit area of Haast Pass; 6, from *Engel 21429*, New Zealand, South Is., Sounds–Nelson EP, Mt. Richmond Forest Park, Red Hills, track to Maitland Hut; 8–10, from *Hatcher 268*, New Zealand, North Is., Northland EP, Waipoua Kauri Forest.)

Jamesoniella colorata (Lehm.) Schiffn.

[Plate 14B, G; Fig. 157]

Jungermannia colorata Lehm., Linnaea 4: 366. 1829. *Jamesoniella colorata* (Lehm.) Schiffn. *in* Engl. & Prantl, Nat. Pflanzenfam. 1 (3, 1): 83. 1893. Lectotype (*fide* Grolle, 1971a): South Africa, Table Mtn., *Ecklon* (S, *non vidi*).

There are no synonyms involving Australasia; for a full synonymy, see Grolle (1971a).

Plants prostrate to erect, the shoot tips slightly ascending, the plants green to (often) reddish, dull, to 1.4 mm wide (broadest in lateral aspect). Branching chiefly ventral-intercalary, with terminal, *Frullania*-type branches rarely present; stolons rarely present. Stems tough, flexuous, becoming light brown, the cortex not distinctly differentiated, of 1(2) layers of slightly smaller cells with strongly thickened walls; medullary cells unevenly thick-walled. Rhizoids from ventral side of stem, extending almost to shoot apex. Leaves mostly laxly imbricate, when dry ± laterally appressed to stem, when moistened obliquely spreading, stiffly vertically oriented, dorsally assurgent, the insertion succubous, recurved at ventral end, the attachment a little less than half the leaf width; leaves 800–1300 μm wide × 800–1400 μm long, orbicular to broadly elliptic, entire (the ventral-apical margin rarely apiculate), shell-like, concave, the margins narrowly inflexed, ± reflexed near the dorsal base, the median-basal portion of the leaf weakly sheathing; apex rounded, rarely somewhat truncate; dorsal margin distinctly decurrent. Cells evenly thick-walled, but in median optical section with thin walls and trigones medium and straight-sided to bulging; cells of upper median portion of leaf ± isodiametric, (12)15–25(30) μm wide and long; median-basal cells larger and somewhat elongated, with knot-like, often confluent trigones, forming an indistinct field; leaf margins often with several rows of cells bleached out and/or thick-walled, the marginal cells with free wall strongly thickened; surface of both leaf surfaces coarsely papillose, the papillae large, high and hemispherical (guttulate), crowded, 3–6(8) per cell, the basal leaf cells coarsely striate-papillose. Oil-bodies 3–5(8) per cell at midleaf, 10–14 per cell at leaf base, 3–5 near leaf margin, finely granular, the surface almost smooth, spherical and 4–6 μm in diam., grading to broadly ellipsoidal and 4–8 × 6–10 μm. Underleaves reduced, united with the ventral leaf margin as a lateral spur or subulate to ciliiform appendage, the uniseriate portion up to 13 cells long, the free margin decurrent on the stem. Fungal partner absent.

Androecia on leading shoots, slightly wider than vegetative sectors, with up to 10 pairs of bracts; bracts strongly saccate in basal portion; lobule sharply inflexed, the apex often apiculate to acuminate, the free margin entire or with 1–2 teeth; antheridia solitary, the stalk biseriate. Gynoecia innovating, notable when young and without a distinct perianth as a tight, ciliate bud; subinvolucral leaves scarcely enlarged, the bracts of innermost series exserted and plainly visible at base of perianth, free from one another, both irregularly laciniate and with accessory lobes, the ultimate divisions ending in a uniseriate row of up to 11 cells, the sinus bases armed with spines; bracteole free or ± broadly united with one of the bracts and of about the same length, dissected as in the bracts. Perianth narrowly oblong (subcylindrical) to fusiform, strongly pleated in the upper 0.25–0.5, strongly contracted to the truncate mouth, the mouth shallowly lobulate, weakly crenulate, the marginal and submarginal cells ± evenly thick-walled and isodiametric or (rarely) ± elongate, usually soon becoming bleached and eroded; cells of perianth proper isodiametric and with moderately thickened walls like the leaf cells; perianth 4–5-stratose in basal ca. 0.3.

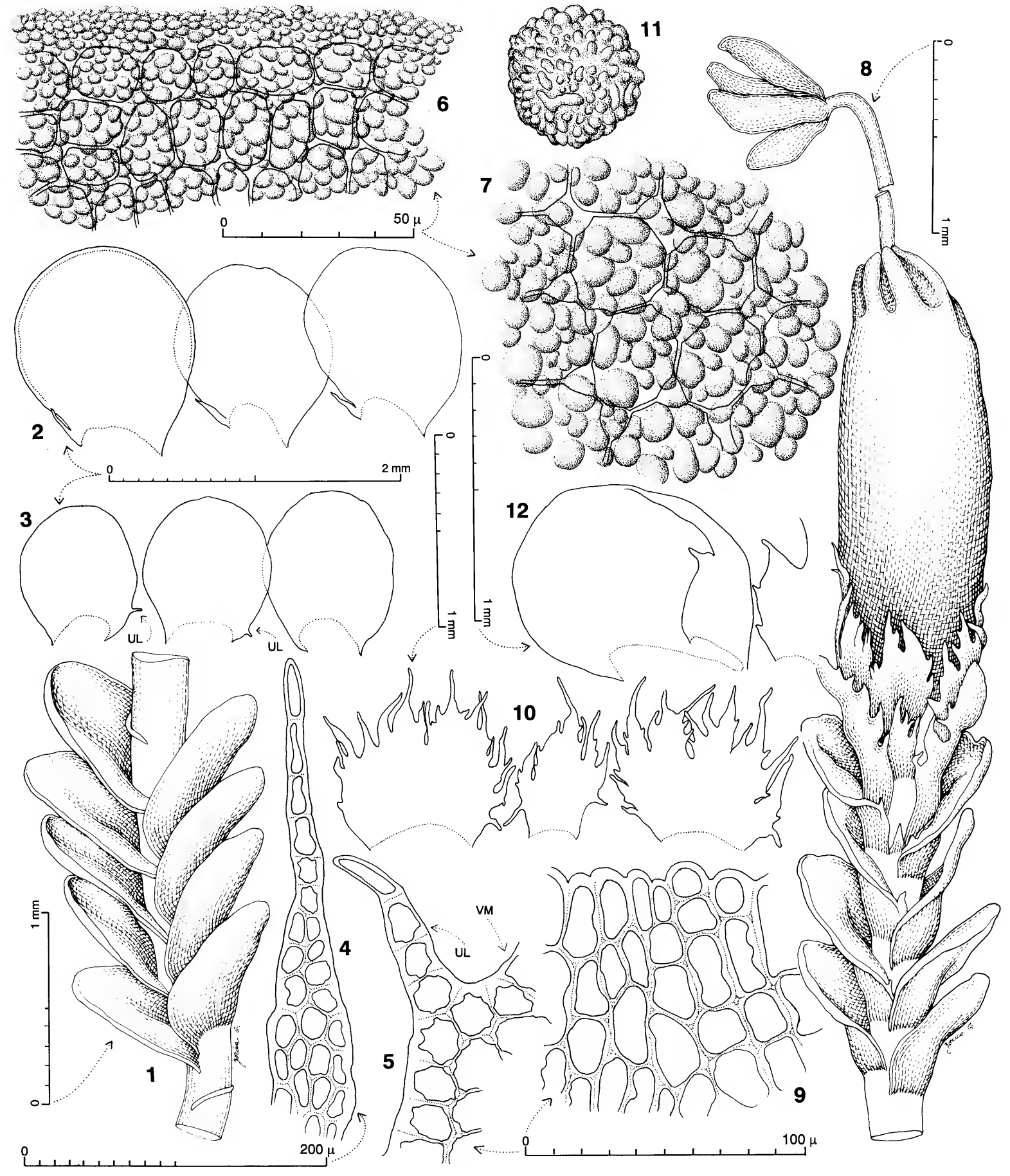

Fig. 157.
Jamesoniella colorata (Lehm.) Schiffn. 1. Sector of main shoot, dorsal-lateral view. 2. Leaves (adaxial face, with united underleaf at left); border of bleached, glistening cells indicated on leaf at left. 3. Leaves (UL = underleaf). 4. Underleaf. 5. Underleaf (= UL) and portion of ventral margin of leaf (= VM). 6. Cells of leaf apex showing guttulate papillae. 7. Upper-median leaf cells showing guttulate papillae. 8. Gynoecium with mature sporophyte, ventral view. 9. Portion of perianth mouth. 10. Innermost ♀ bracts and, in middle, bracteole. 11. Spore (× 1070). 12. ♂ Bract and, to right, a lobule of second bract. (Figs. 1, 3, 5, 6, 8–12, from *Hatcher 943*, New Zealand, South Is., Fiordland EP, N side of McKerrow R., Martins Bay; 2, 4, 7, from *Engel 21964*, New Zealand, South Is., Fiordland EP, Gertrude Valley.)

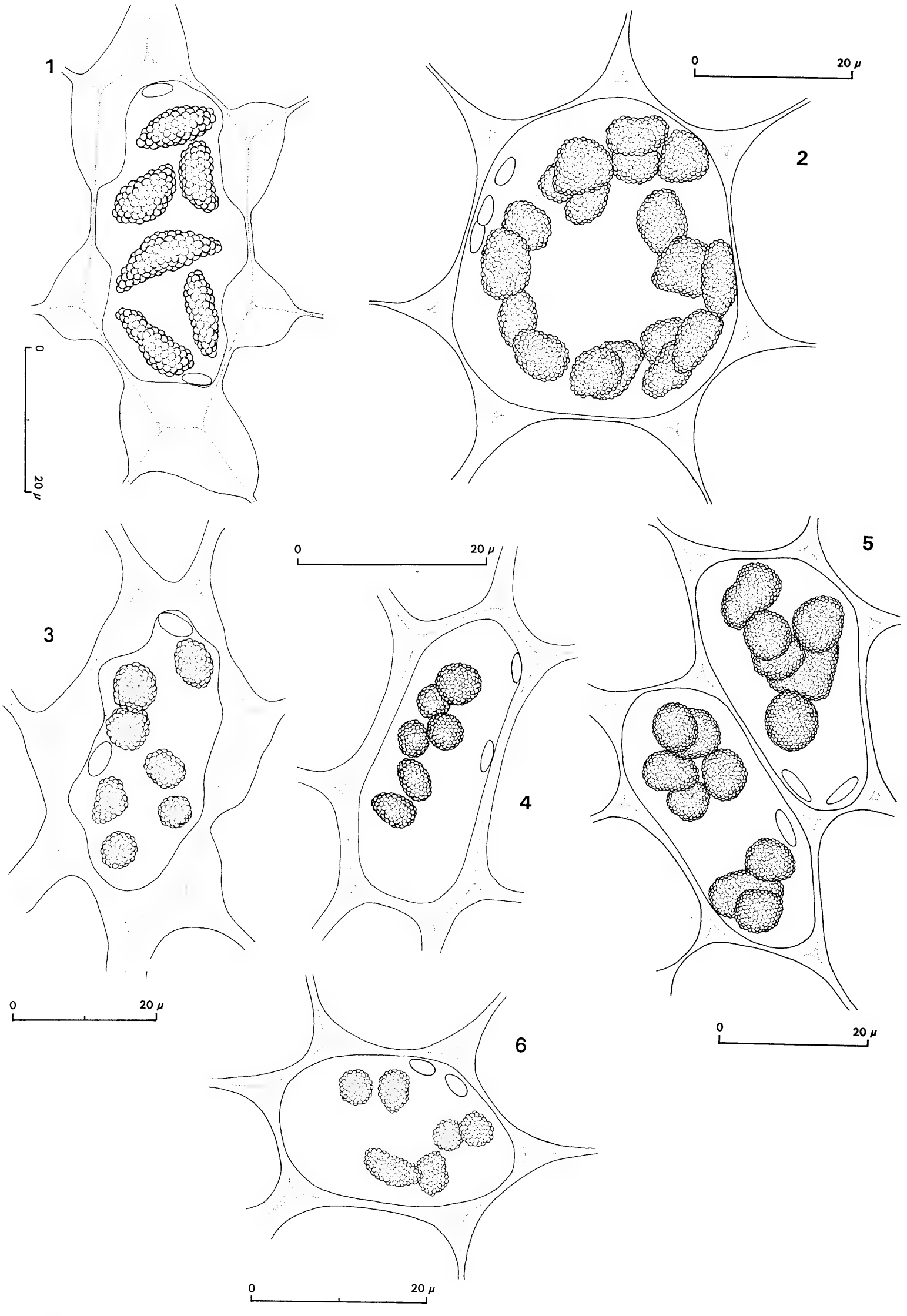

Fig. 158.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Jamesoniella kirkii* Steph. Median leaf cells. 2. *Jamesoniella tasmanica* (Hook.f. & Taylor) Steph. Median leaf cells. 3. *Cuspi-*

Capsule ellipsoidal, the wall 35–45 μm thick, 5-stratose; outer layer of cells with the radial longitudinal walls with nodular thickenings, the thickenings of adjoining cells often in opposing pairs; innermost layer of cells with thickened longitudinal walls, with semiannular bands common, rather wide, complete or occasionally tapering before reaching the opposite wall.

Spores 18.2–22 μm in diam., verrucate (coarsely and irregularly warty). Elaters bispiral, 7.2–8.6 μm wide.

Distribution and Ecology: Pan-south-temperate including New Zealand: Campbell Island, Auckland Islands (150–640 m), Antipodes Islands (300–370 m), Stewart Island (500–695 m), South Island (230–1530 m), North Island (290–1700 m); Australia: Macquarie Island, Tasmania, southeast Australia; Falkland Islands; southern South America; Tristan da Cunha; Inaccessible Island; Africa (South Africa, Natal, Transvaal); Marion Island; Prince Edward Island; Crozet Island; Kerguelen Island. With a distribution similar to *Cryptochila grandiflora* of the same family, but unlike that species *Jamesoniella colorata* has not penetrated north beyond temperate regions in any of the sectors. In New Zealand known from Fiordland, Southland, Otago, Westland, Canterbury (including Banks Peninsula), Western Nelson, Sounds–Nelson, Marlborough, Southern North Island, Volcanic Plateau, Taranaki (Mt. Taranaki), Gisborne and Auckland (Rangitoto Island, Mt. Moehau) EPs.

The species occurs in upper-elevation forests and in the penalpine–alpine zones, particularly where there is exposure. It often is saxicolous, particularly where a thick layer of soil has accumulated over rock, or terricolous, and rather frequently occurs with *Cuspidatula monodon*. It is occasional at lower elevations, such as on roadside banks at ca. 480–650 m, ca. 3 km east of Te Aroha. Also on small upper tree branches, such as *Weinmannia*, occurring, for example, with *Pseudomarsupidium piliferum* at 950 m in a stunted mixed-age *Nothofagus menziesii* forest with *Weinmannia* and *Ixerba brexioides* codominant (Mt. Te Aroha). It has a curious presence on Rangitoto Island (Auckland, 50–160 m), occurring on thick soil over lava rock in a *Metrosideros* forest over the lava flow. At that site it occurs with several other taxa that typically occur at higher elevations, such as *Cuspidatula monodon*. Other species that occur with *Jamesoniella colorata* are *Anastrophyllum schismoides*, *Andreaea acutifolia*, *A. acuminata*, *Campylopus clavatus*, *Categonium nitens*, *Cladia aggregata*, *C. retipora*, *Cladonia confusa*, *Conostomum pentastichum*, *Cryptochila acinacifolia*, *Diplophyllum domesticum* var. *icari, Ditrichum punctulatum*, *Frullania rostrata*, *Goebeliella cornigera*, *Hypnum cupressiforme*, *Isotachis intortifolia*, *Racomitrium crispulum*, *R. pruinosum*, *Rhacocarpus purpurascens*, *Siphula fragilis* and *Stereocaulon ramulosum*.

Comments: The species may be recognized most readily by the coarse, crowded, high and hemispherical (guttulate) papillae, only 3–6(8) per cell at midleaf (Fig. 157: 6, 7). The aspect of the plant is also distinctive, the leaves are stiffly vertically oriented and have the same shell-like, concave appearance when wet or dry (Plate 14: B, G; Fig. 157: 1). Older plants or speci-

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datula monodon (Hook.f. & Taylor) Steph. Upper-median leaf cells. 4, 5. *Cryptochila grandiflora* (Lindenb. & Gottsche) Grolle. Median leaf cells. 6. *Cryptochila pseudocclusa* (E.A.Hodgs.) R.M.Schust. Median leaf cells. (Fig. 1, from *Glenny 9102*, New Zealand, South Is., Westland EP, Mt. Brown; 2, from *Glenny 9232*, New Zealand, South Is., Nelson, Takaka Hill, Harwoods Hole Track; 3, from *Glenny 9127*, New Zealand, South Is., Nelson, Mt. Burnett; 4, from *Glenny 9089*, New Zealand, South Is., Canterbury EP, Mt. Aicken; 5, from *Glenny 9592*, New Zealand, South Is., Western Nelson EP, Stockton Plateau; 6, from *Engel 27179*, New Zealand, South Is., Western Nelson EP, Kahurangi Natl. Park, vicinity of Gordon's Pyramid.)

mens in poor condition may have the papillae eroded and indistinct. In such cases, the presence of trigones will distinguish this species from *Cryptochila grandiflora*. For additional differences between these species, see comments under the latter. *Cryptochila nigrescens* is similar in aspect, but can be distinguished from *Jamesoniella colorata* by the interlocking dorsal leaf bases (Fig. 161: 1) and the absence of surface papillae.

Cuspidatula Steph.

Cuspidatula Steph., Sp. Hepat. 2: 124. 1901.

Plants rigid, prostrate, with ascending tips, light green to ± brown to purplish brown or reddish, nitid, medium-sized, to 2.5 mm broad. Branching sparse or rather common, irregular, the branches all or in part ventral-intercalary, evidently from ventral ends of lateral merophytes; *Frullania*-type branches also present in *Cuspidatula contracta* and at least at times in *C. monodon*. Stem wiry, with cortex in 1(2) layers of rigid, thick-walled cells; medullary cells larger, strongly thick-walled. Rhizoids frequent, scattered. Leaves widely spreading when moist, often dorsally ± connivent in drying, closely imbricate, asymmetrical to nearly symmetrical, ovate to ovate-lanceolate, unlobed, apices acute to short-acuminate or piliferous (occasionally obtuse to rounded in *C. contracta*), edentate; dorsal margin straight to arched, entire, the ventral arched, subcordate at the base, entire, exceptionally with a tooth. Cells in median sector mostly hexagonal to hexagonal-oblong, with strongly nodose trigones and conspicuous middle lamella; surface smooth or striate-papillose. Oil-bodies (*C. monodon*) 5–10 per cell, moderately botryoidal. Underleaves absent or vestigial, of 1–2 segments formed of 1–2 elongated cells, each ending in an ephemeral slime papilla. Asexual reproduction lacking (?or by fragmentation of leaf apices).

Dioecious. Androecia (data from *Cuspidatula monodon*) on leading shoots, rather inconspicuous, becoming intercalary; bracts somewhat smaller than leaves, the base ventricose, the distal sector tapering and similar in form to leaves; lobule margin involute, distinctly long-acuminate distally; antheridia 1 per bract, the stalk biseriate; paraphyllia lacking. Gynoecia terminal on leading leafy shoots or relatively short gynoecial innovations; bracts large, the insertion distinctly narrow, the bracts 2–4-lobed to 0.4–0.65, the lobes narrow, obtuse or long-acute to acuminate to caudate-piliferous, the lobe margins sparingly dentate-laciniate or entire, the lamina subentire or with a few small teeth or laciniae; bracteole free or narrowly connate on 1 side, smaller than bracts, oblong-lanceolate, undivided and distally acute or acuminate, on each side with a ciliiform to lobuliform process + a few small teeth, the bracteole at times bifid to ca. 0.5 in *C. contracta*. Perianths ovoid-cylindrical or oblong-obovate, terete basally, deeply plicate distally, the perianth moderately contracted toward the mouth; mouth irregularly lobulate, fringed with stiff, piliferous cilia.

Sporophyte known only for *Cuspidatula monodon*. Seta relatively short to rather long, of numerous, cells, the outer 1 (locally 2) rows of cells considerably smaller than the internal cells. Capsule ellipsoidal–narrowly ovoid, the wall 3–4-stratose, 23–30 μm thick; outer layer of cells notably small, subquadrate to short-rectangular, the walls uniformly hyaline, devoid of sheet-like thickenings, the radial longitudinal and transverse walls devoid of nodular thickenings or with at most 2, feebly pigmented, mostly low nodules; innermost cells irregularly long-rectangular (at times markedly so), with walls very thin, uniformly hyaline, devoid of sheet-like thickenings, with nodular thickenings that "trail off" onto the outer tangential wall

as feebly pigmented, spur-like extensions, with opposing spurs at times approaching, but only exceptionally with complete semiannular bands.

Spores pale yellowish brown, 13.9–16.3 μm in diam. (including bacula), baculate, the bacula well-separated and truncate at the summit. Elaters somewhat tortuous, 5.8–7.7 μm wide, bispiral to tips, the spirals tightly wound, 1.9–2.4 μm wide.

Lectotype (*fide* Grolle, 1971a): *Cuspidatula contracta* (Reinw., Blume & Nees) Steph.

A genus with two species: *Cuspidatula monodon*, which is widely distributed in temperate Australasia, and *C. contracta* (Reinw., Blume & Nees) Steph. of New Guinea, Java, Sumatra, Philippines, Thailand, Amboina, Samoa, Tahiti, Fiji, Mauritius, Seychelles and Tanzania. Grolle (1971a) placed *C. caledonica* Steph. in the synonymy of *Acrochila caledonica* (Steph.) Inoue.

Kitagawa (1981) and Glenny (1998) treated *Cuspidatula* as a synonym of *Jamesoniella*; they are treated as discrete genera here, differing not only in sterile gametophytic characters, but in features of the androecium and sporophyte, as follows:

1a. Leaves strongly tapered and sharp; ♀ bracts deeply 2(3)-fid to 0.45–0.6 (Fig. 160: 2); ♂ bract lobule distinctly long-acuminate distally (Fig. 160: 9, 10); seta with outer 1 (locally 2) row(s) of cells considerably smaller than the internal cells; outer layer of capsule wall cells with nodular thickenings lacking, or, if present, low, feebly pigmented and 2 or less per radial wall (Fig. 160: 6); innermost layer of capsule wall cells with nodular to feebly pigmented, spur-like thickenings, only exceptionally with complete semiannular bands (Fig. 160: 7) . . . . . *Cuspidatula*

1b. Leaves rounded at the summit; ♀ bracts never deeply 2–3-fid; ♂ bract lobule margin at times a tooth; seta with ± equal-sized cells; outer layer of capsule wall cells with strong nodular thickenings; innermost layer of capsule wall cells with well-developed semiannular bands . . . . . *Jamesoniella*

References: Hodgson (1946); Schuster (2002a).

Cuspidatula monodon (Hook.f. & Taylor) Steph.

[Plate 12D; Fig. 158: 3, oil-bodies, p. 724; Figs. 159, 160]

Jungermannia monodon Hook.f. & Taylor, London J. Bot. 3: 559. 1844; Taylor *ex* Lehm., Nov. Min. Cogn. Stirp. Pug. 8: 7. 1844. *Anastrophyllum monodon* (Hook.f. & Taylor) Steph., Hedwigia 32: 140. 1893. *Cuspidatula monodon* (Hook.f. & Taylor) Steph., Sp. Hepat. 2: 126. 1901. *Jamesoniella monodon* (Hook.f. & Taylor) N.Kitag., Bull. Nara Univ. Educ. 30: 47. 1981. Type: Tasmania, 1824, *Spence* ("Hb. Greville et Taylor").

Jungermannia geminiflora Colenso, Trans. & Proc. New Zealand Inst. 20: 243. 1888 (1887). Type: New Zealand, North Is., Waipawa Co., S of Dannevirke, 1887, *Colenso*.

Jungermannia consimilis Colenso, Trans. & Proc. New Zealand Inst. 21: 47. 1889 (1888). Type: New Zealand, North Is., Waipawa Co., S of Dannevirke, 1888, *Colenso*.

Plants rigid, prostrate, the tips ascending, greenish brown to golden brown to purplish brown to reddish, nitid when dry, medium-sized, to 2.5 mm broad, rather short, seldom exceeding 2 cm long. Branching rather common, irregular, the branches all or in part ventral-intercalary, evidently from ventral ends of lateral merophytes (superficially appearing ventral in origin); *Frullania*-type branches rather common in some populations, apparently lacking in others, the

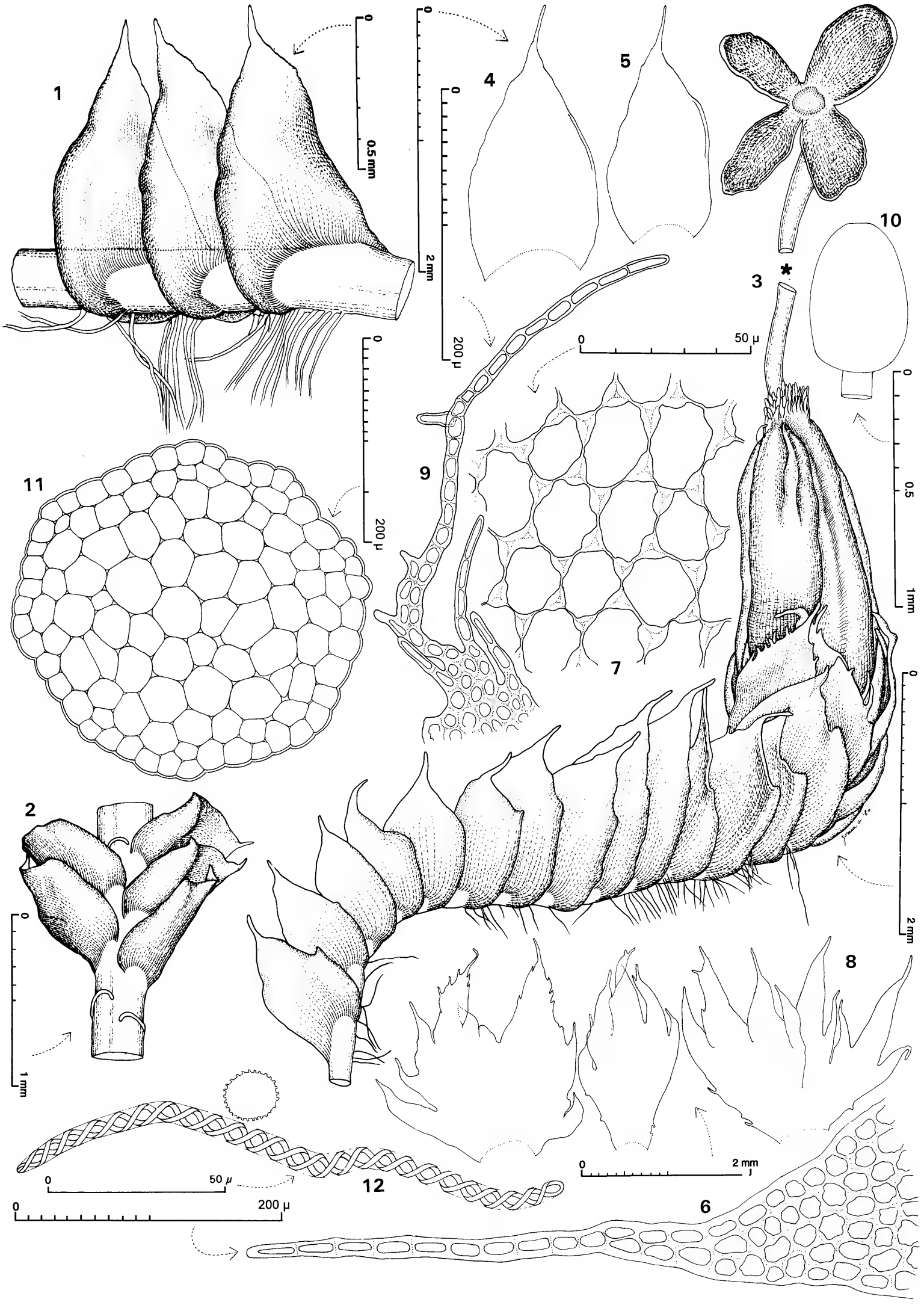

Fig. 159.
Cuspidatula monodon (Hook.f. & Taylor) Steph. 1. Sector of shoot, lateral view. 2. Sector of shoot, ventral view; note very narrow ventral merophytes. 3. Shoot with mature sporophyte. 4, 5. Leaves, ventral margin to right. 6. Portion of leaf apex. 7. Median leaf cells. 8. ♀ Bracts and, in middle,

half-leaf of similar form to the leaves, broadly connate with the first branch underleaf, which is ovate and broadly rounded at the summit. Stem wiry, with cortex in 1(2) layers of rigid, thick-walled cells, the exposed wall pigmented, notably thickened; medullary cells larger, strongly thick-walled with distinct, bulging corner thickenings. Rhizoids whitish, frequent, scattered. Leaves typically dorsally ± connivent in drying, when moist strongly dorsally assurgent grading to widely spreading, closely imbricate, 570–1100 μm wide × 750–1650 μm long, often adaxially concave, symmetrically to asymmetrically ovate-lanceolate, unlobed, apices caudate-piliferous, terminating in a uniseriate row of 8–15 cells, the distal cells highly elongated (to 8:1), otherwise entire, the tips often appearing hyaline and parched; dorsal margin arched and rather similar to the ventral in degree curvature (the leaves then symmetric) or the dorsal margin straight (the leaves then asymmetric), the ventral margin always arched, often sharply and locally incurved, entire but often a small blunt projection in distal portion of median third of margin, the base subcordate. Cells in median sector with strongly nodose trigones, the middle lamella conspicuous, 20–24 μm wide × 25–31 μm long; surface striate-papillose or smooth. Oil-bodies in all cells of leaf except distal cells of uniseriate row of leaf tips, occupying conspicuous portion of cell lumen, hyaline, glistening, 3(5)–(7)10 per cell, moderately botryoidal, subglobose and 4–6 μm in diam. to ellipsoidal, sometimes crescent-shaped and 5–7 × 9–12 μm. Chloroplasts large for cell size. Underleaves absent or vestigial, of 1–2 segments formed of 1–2 elongated cells, each ending in an ephemeral slime papilla; ventral merophytes appearing to be 2–3 cells broad. Asexual reproduction lacking (?or by fragmentation of leaf apices). Fungal partner absent.

Dioecious. Androecia on leading shoots, rather inconspicuous, becoming intercalary, often repeatedly so, ± spicate; bracts in 4–6 pairs, somewhat smaller and (when moist) more dorsally assurgent than leaves, the distal sector tapering and similar in form to leaves; lobule well developed, inflated, rather large for bract size, with a short, low wing, the free margin involute, distinctly long-acuminate distally; antheridia 1 per bract, the stalk biseriate, the stalk cells thick-walled; paraphyllia lacking. Gynoecia terminal on leading leafy shoots or relatively short gynoecial innovations; bracts large, sheathing the perianth, rather deeply concave, the insertion markedly narrow, the innermost pair of bracts often differing in lobe number, one bilobed, the other 3–4-lobed, in either case divided to 0.4–0.65, the lobes long-attenuate to acuminate to caudate-piliferous, terminating in a uniseriate row of up to 10 cells, the distal cells often elongated (to ca. 4:1), the lobe margins entire or with several often opposing sharp teeth and accessory lobule(s), the lamina on each side with a few small teeth and often an attenuated lobule; bracteole free or narrowly connate on 1 side, less than 0.55 width of bracts, distinctly narrow at the insertion, usually shorter than the bracts, oblong-lanceolate, acute or acuminate, undivided, on each side usually with a ciliiform to laciniiform to lobuliform process in distal half, the lateral processes never exceeding the length or size of the main, median process, the lamina also with a few small teeth and at times an accessory lobule below. Perianths frequent,

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bracteole. 9. Portion of perianth mouth. 10. Capsule profile. 11. Seta, cross section. 12. Elater and spore profile at same scale. (Figs. 1, 2, 7, from *Engel 12855*, Tasmania, Arve Valley; 3, from *Engel 16020*, Tasmania, West Downs; 4–6, from *Engel 24907*, New Zealand, South Is., Westland EP, Lake Kaniere Scenic Reserve, Lake Kaniere; 8, from *Engel 23606*, New Zealand, North Is., Auckland EP, Kaimai Ra., spur ESE of Ngatamahinerua; 9, from *Engel 13155*, Tasmania, Tasman Peninsula; 10, 12, from *Engel 23541*, New Zealand, North Is., Auckland EP, Kaimai Ra., Aongatete network of tracks at the end of Wrights Road off Katikati–Tauranga highway; 11, from *Engel 18000*, New Zealand, South Is., Westland EP, summit area of Haast Pass.)

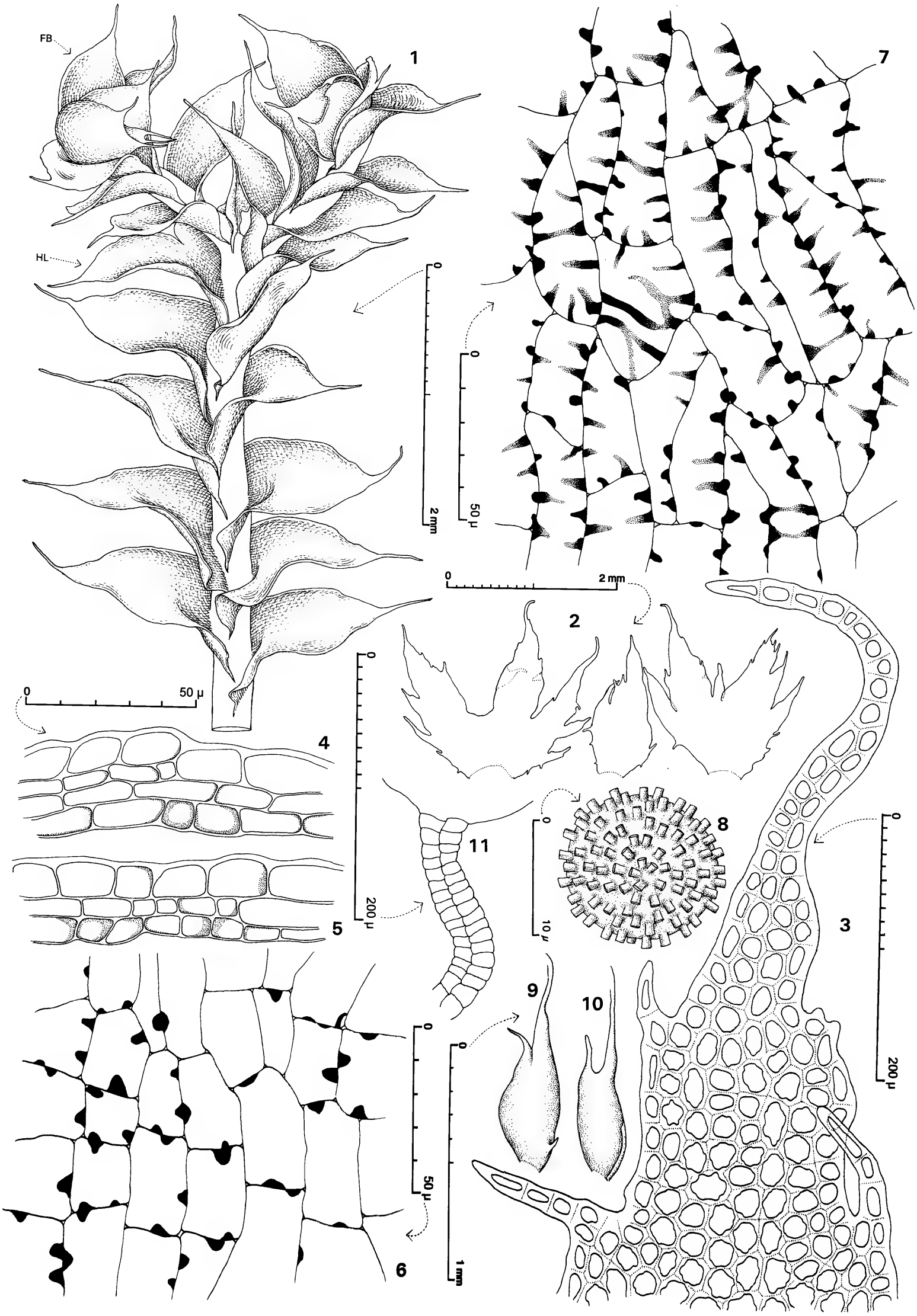

Fig. 160.
Cuspidatula monodon (Hook.f. & Taylor) Steph. 1. Sector of shoot with *Frullania*-type branch (= FB) (dorsal view). Note that the half-leaf (= HL) is distinctly connate with the first branch underleaf.

large for shoot size, terete and ± inflated basally, the distal 0.6–0.7 deeply plicate, the plicae 5–7, rounded, separated by deep sulci, contracted at the often scorched mouth; mouth lobulate and ciliate/laciniate with stiff, piliferous cilia that terminate in a uniseriate row of 9–17 elongate, thick-walled cells, the lacinia bases often with a few, often opposed, stiff teeth.

Sporophyte as in generic description.

Distribution and Ecology: New Zealand: Auckland Islands (400 m), Antipodes Islands (200–300 m), Stewart Island (10–100 m), South Island (5–1525 m), North Island (60–1200 m), Chatham Islands (140–240 m); Australia: Tasmania, Victoria, New South Wales. Known from all ecological provinces of New Zealand. Extending to drier parts of some provinces, e.g., present in Marlborough (Pelorus Valley, Mt. Robertson), Banks Peninsula, Hawkes Bay and Wairarapa.

A common species throughout our area, but typically in rather exposed sites. It occurs on tree bark, e.g., on *Nothofagus* spp., *Agathis australis* (where particularly common), *Phyllocladus*, *Weinmannia*, *Metrosideros*, *Coprosma* and *Libocedrus*. Also on the bark of a number of species of *Dracophyllum*, e.g., in an area of rocky outcrops and shrub-heath communities including *Coprosma foetidissima*, *Corokia buddleioides*, *Dracophyllum recurvum*, *Lepidothamnus laxifolius* and *Oreobolus pectinatus* (exposed rocky ridge below summit area of "Little Moehau," Mt. Moehau, Coromandel Forest Park, ca. 800–840 m). In "mesic conditions" also on old rotted, often decorticated logs. Commonly found on soil in rock crevices, particularly on exposed rock outcrops but also under forest. Also found on peat in penalpine bogs at sites subject to strong surface drying, and on soil, decomposing litter, and shrub bases in penalpine tussockland and scrub. Found with *Campylopus introflexus*, *Hypnum cupressiforme*, *Jamesoniella colorata*, *Lepidozia obtusiloba*, *Leptotheca gaudichaudii*, *Pseudomarsupidium piliferum*, *Ptychomnion densifolium*, *Racomitrium crispulum*, *R. lanuginosum* and *R. pruinosum*.

The species is strikingly tolerant of desiccation and may occur under quite rigorous conditions. For example, it was found on a thick soil layer over rock with *Pseudomarsupidium piliferum* over a lava flow within a forest of *Metrosideros robusta* (Rangitoto Island, 50–160 m). Also in the frost flats near Otupaka Stream (SW of Minginui, 700 m), a rigorous environment consisting of an open, low area with scattered *Leptospermum scoparium* and *Dracophyllum subulatum* with abundant *Cladonia*. And in the alpine zone it may form tight clumps on ice-eroded banks (below and W of Mt. Armstrong, SSW of Mt. Brewster, Mt. Aspiring Natl. Park, 1250–1450 m). The species may be a frequent component of the tree canopy bryoflora, and Allison and Child (1975, p. 94) mentioned that the species is "frequently an epiphyte, on branches rather than trunks." Hodgson (1946, p. 73) indicated "K. W. Allison has a note to the

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2. ♀ Bracts and, in middle, bracteole. 3. Distal sector of ♀ bract lobe. 4, 5. Capsule wall, cross sections (both drawn to same scale). 6. Capsule wall, outer layer. 7. Capsule wall, inner layer. 8. Spore. 9, 10. Lobules of ♂ bracts, note short spur or wing at arrows. 11. Antheridial stalk. (Fig. 1, from *Engel 24907*, New Zealand, South Is., Westland EP, Lake Kaniere Scenic Reserve, Lake Kaniere; 2, 3, from *Engel 23606*, New Zealand, North Is., Auckland EP, Kaimai Ra., spur ESE of Ngatamahinerua; 4–8, from *Engel 23541*, New Zealand, North Is., Auckland EP, Kaimai Ra., Aongatete network of tracks at the end of Wrights Road off Katikati–Tauranga highway; 9–11, from *Engel 23998*, New Zealand, North Is., Gisborne EP, Urewera Natl. Park, Huiarau Ra., summit area of Te Rangaakapua.)

effect that this species is sometimes found growing in the tops of tall forest trees." Moreover, it may be found in fallen masses of bryophytes on the forest floor, e.g., in a mixed broadleaf forest dominated by *Beilschmiedia* and *Vitex lucens*, with *Rhopalostylis sapida*, *Coprosma*, *Dacrycarpus dacrydioides* and *Hoheria* (Kiwanis Reserve, N edge of Herekino Forest area, Northland, ca. 60–80 m). When found epiphytically, typical accompanying species are *Acrochila biserialis*, *Dicnemon calycinum*, *D. semicryptum*, *Frullania aterrima*, *Holomitrium perichaetiale*, *Macromitrium longipes*, *Paraschistochila tuloides*, *Porella elegantula*, *Pseudomarsupidium piliferum*, *Pyrrosia eleagnifolia*, *Usnea rubicunda* and *Weymouthia cochlearifolia*.

Comments: This species may be readily recognized in the field by the closely imbricate, unlobed leaves with the apex caudate-piliferous (Fig. 159: 1, 4, 5; Fig. 160: 1). It has been confused with *Chandonanthus squarrosus*, which can be a similar red or brown color, is found in similar habitats and has acute leaf lobe apices, but *Chandonanthus* has bifid leaves. The leaves, when moist, are often strongly dorsally assurgent (Fig. 159: 1), but may be widely spreading (Fig. 160: 1), and in some cases populations are either of one type of leaf orientation or the other. Leaves are typically dorsally ± connivent in drying. Plants are greenish brown to golden brown or reddish, prostrate, and often form pure, quite large patches. Underleaves are completely lacking, and ventral merophytes are very narrow (Fig. 159: 2). Schuster (2002a, p. 411, 413) was unable to document *Frullania*-type branches for the species. We have found that terminal branching is rather common in some populations of *Cuspidatula monodon* (Fig. 160: 1) while apparently lacking in others.

Spores are baculate and the bacula are truncate at the summit (Fig. 160: 8). This is yet another example of a predominantly corticolous hepatic having baculate spores (for a discussion see Engel and Gradstein, 2003).

Cryptochila R.M.Schust.

Cryptochila R.M.Schust. J. Hatt. Bot. Lab. 26: 284. 1963.

Plants erect, deep green or reddish brown to fuscous, often nitid, vigorous, to 2.5 mm wide and 10 cm long, clearly divided into a system of rhizoidous leafless stolons and stiffly erect or ascending leafy shoots of determinate height. Branching sparing, the branches ventral-intercalary; *Frullania*-type branching lacking (sporadic on ♂ plants in *Cryptochila pseudocclusa*); stoloniform branches frequent, strongly geotropic, originating just above point of origin of leafy, phototropic branches. Stems rigid, with 2–3(4) strata of thick-walled, brown to fuscous (at maturity) cells smaller in diameter than medullary cells; paraphyllia often present, vestigial. Rhizoids scarce, usually restricted to stolons. Leaves alternate, often subvertical, erect to widely spreading, transversely oriented, inserted on an asymmetric, acroscopically convex line, undivided and entire, the apex rounded. Cells in median sector often hexagonal, the walls firm, evenly thick-walled and lacking trigones or with trigones large and bulging (but not nodulose); peripheral sectors of leaves with cells mostly subquadrate, with walls evenly thick-walled; median-basal cells elongated (ca. 2–4:1), evenly thick-walled or with coarse trigones; surface smooth, except sometimes basally (often delicately striate-papillose in *C. grandiflora*). Oil-bodies 2–12 per cell, finely to coarsely papillose, at times lacking in marginal/submarginal cells. Underleaves vestigial, consisting of an ephemeral cilium or 2–4 such cilia, or a filiform rudiment often connate at base with a lateral leaf. Asexual reproduction absent.

Dioecious. Androecia eventually intercalary, with 4–5 or more pairs of bracts, the bracts smaller than leaves, the dorsal margin with or without a discrete lobule; paraphyllia often present; antheridia 1 per bract, the stalk 2-seriate. Gynoecia often innovating, the innovations repeatedly gynoecial; subinvolucral bracts leaf-like, but distal 2(3) series of bracts progressively smaller, in inner gyre one bract often much reduced; innermost bracts polymorphic, often unequal in size, coarsely dentate/lobulate at least basally, free, ventrally often with 1–2 coarse lobes; bracteole free or nearly so, similarly polymorphous, often bilobed and toothed/laciniate, to 0.65–0.9 length of bracts. Perianth long-emergent at maturity, contracted to the deeply (5)6–12-plicate mouth, distally often twisted; mouth weakly crenulate or entire; perianth 2–several-stratose in basal half, firm.

Capsule ellipsoidal, the wall thick, of 5–7 layers; outer layer of cells ca. 2× height of each inner stratum, with well-developed nodular thickenings; innermost layer of cells with mostly nodular to spine-like thickenings, the thickenings only sporadically extending across tangential wall to form complete semiannular bands.

Spores finely and closely papillose, the papillae often forming short-vermiculate ridges. Elaters bispiral.

Type: *Cryptochila pseudocclusa* (E.A.Hodgs.) R.M.Schust. (≡ *Jamesoniella pseudocclusa* E.A.Hodgs.)

A genus of six species, all south temperate in distribution. One species, *Cryptochila grandiflora*, extends north in the Andes at high elevations, north into Central America and in southeast Brazil. Grolle (1971a) divided the genus into three subgenera:

1) subg. *Nigritula* Grolle, with only *C. nigrescens* of our area;

2) subg. *Cryptochila*, with *C. pseudocclusa* of our area and *C. grandiflora*, a pan-south-temperate species;

3) subg. *Acinaria* Grolle, which is comprised of two sections, sect. *Acinaria*, with *C. acinacifolia* of our area and *C. paludosa* (Steph.) Grolle of the Falkland Islands, southern South America and Tristan da Cunha, and sect. *Spegazzinia* Grolle, with *C. spegazziniana* (Spruce) Grolle of southern South America.

References: Grolle (1971a); Schuster (1970b, 2002a).

Key to Species

1a. Lateral merophytes not interlocking; leaf cells evenly thick-walled (at least in distal portion of leaf) 2
  2a. Dorsal leaf base unistratose; leaves orbicular to reniform, ventrally secund; stem paraphyllia usually present 3
    3a. Dorsal leaf margins erect-inflexed to involute . . . . . *C. grandiflora* (p. 736)
    3b. Dorsal leaf margins sharply and narrowly revolute . . . . . *C. pseudocclusa* (p. 740)
  2b. Dorsal leaf base 2–3-stratose at and above the insertion; leaves lingulate, dorsally assurgent; stem paraphyllia lacking . . . . . *C. acinacifolia* (p. 742)

1b. Lateral merophytes interlocking, the leaf insertions distinctly crossing the stem midline dorsally; leaf cells thin-walled, with distinct trigones . . . . . *C. nigrescens* (p. 734)

Cryptochila nigrescens (Steph.) Grolle

[Fig. 161]

Jamesoniella nigrescens Steph., Hedwigia 34: 48. 1895. *Cryptochila nigrescens* (Steph.) Grolle, Feddes Repert. 82: 15. 1971. Type: New Zealand, Great Barrier Is., *Kirk 87*.
Jamesoniella patula Steph., Hedwigia 34: 48. 1895. Lectotype (*fide* Grolle, 1971a): New Zealand, Te Whau, *Kirk 537* (G, *non vidi*); isotypes: (CHR 4879!, CHR 4899!).

Plants erect-ascending from a prostrate leafless axis (or prostrate in thin mats on sandy soil), firmly anchored by stolons, reddish to reddish brown, to 1.5 mm wide. Stems rigid, becoming brownish, the cortical cells in 2–3 layers of thick-walled, colorless to moderately brownish cells; medullary cells thin-walled, colorless. Paraphyllia short-filamentous to scale-like, sparsely

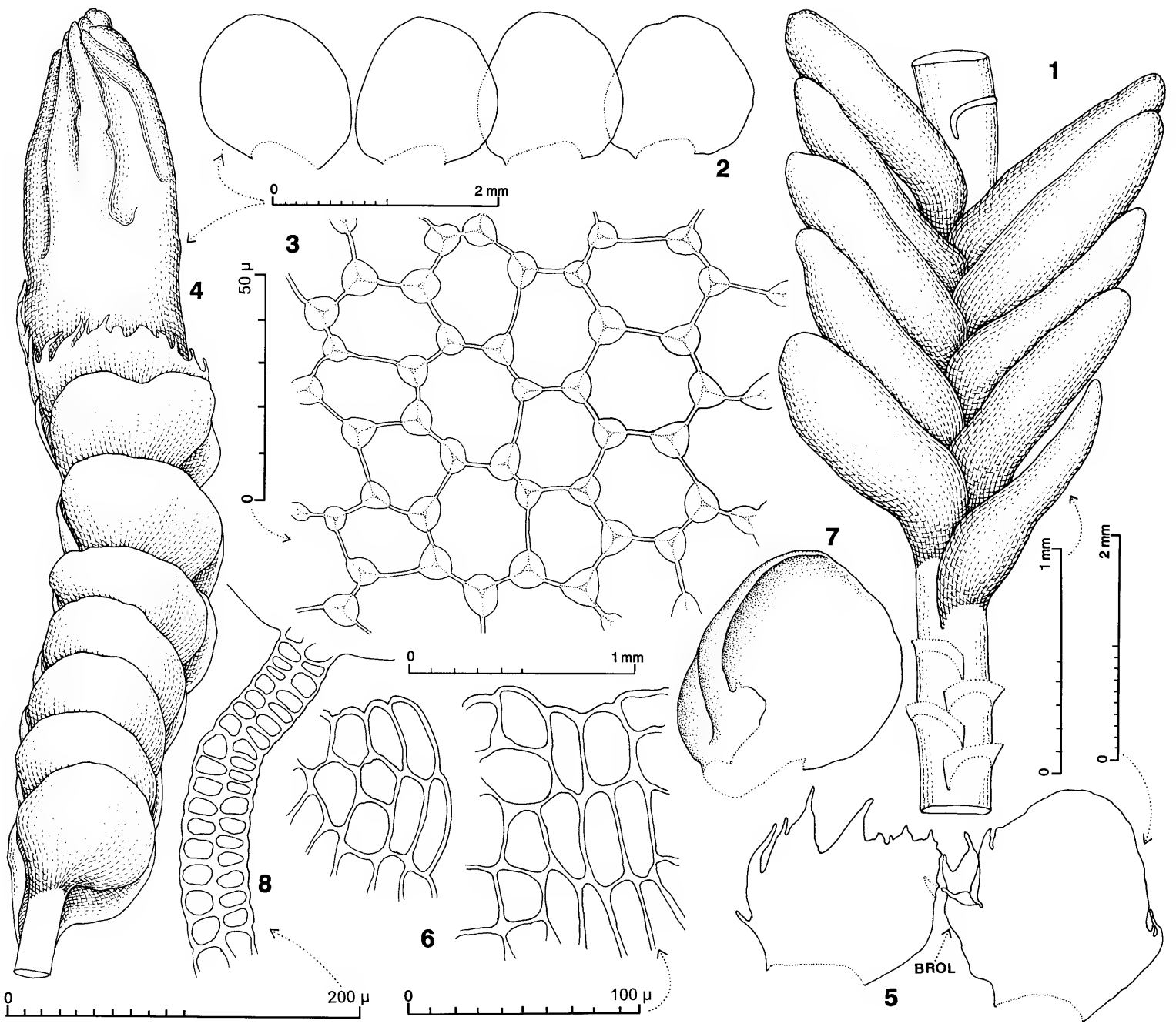

Fig. 161.
Cryptochila nigrescens (Steph.) Grolle. 1. Sector of shoot showing interlocking leaf insertions, dorsal view. 2. Leaves. 3. Upper median leaf cells. 4. Mature gynoecium, lateral view. 5. Innermost ♀ bracts and, in middle, bracteole (= BROL). 6. Portions of perianth mouth. 7. ♂ Bract. 8. Antheridial stalk. (Figs. 1, 4–6, from *Engel 19273*, New Zealand, South Is., Western Nelson EP, Paparoa Ra., N side of Tiropahi R., W side of Highway 6 ca. 500 m N of bridge over R.; 2, 3, 7, 8, from *Engel 19272*, same loc.)

present on dorsal side of stem between the leaves (at least on robust shoots). Rhizoids sparse, frequently confined to stolons, at times also on ventral side of normal leafy shoots (on prostrate shoots). Branching exclusively ventral-intercalary, in sterile sectors nearly exclusively basal; microphyllous stolons sporadically present. Leaves imbricate, vertically oriented, shell-like, concave, when dry loosely appressed to the stem, when moist obliquely spreading from a short-sheathing base, the insertion transverse to weakly succubous, distinctly crossing the midline dorsally; leaves broadly elliptic to orbicular (at times ovate with a subcordate base), 1000–2250 μm wide × 1100–1750 μm long, entire, contracted to the base, the apex broadly rounded to (rarely) retuse; dorsal margin usually distinctly inflexed, moderately arched, not or slightly decurrent; ventral margin plane, moderately to distinctly arched, often contracted to base, short-decurrent. Cells in indistinct concentrically aligned rows, quadrate to short-rectangular, thin-walled, with distinct, medium and straight-sided to bulging to knot-like trigones; cells of median portion of leaf 20–24(27) μm wide × 27–35 μm long; median-basal cells somewhat elongate, but not forming a sharply demarcated field; surface smooth or finely and delicately but somewhat remotely papillose lending a "speckled" appearance, the basal cells faintly longitudinally striate-papillose. Underleaves absent or uniseriate, filamentous and caducous; ventral merophyte row very narrow.

Androecia on leading shoots, of similar width to vegetative sectors, with up to 8 pairs of bracts; bracts saccate in basal portion; lobule weakly developed, inflexed, semicircular, the free margin entire; antheridia solitary, the stalk biseriate, the stalk cells very thick-walled. Gynoecia usually not innovating, the bracts not much larger than vegetative leaves, those of innermost series of similar size to those below, free from one another, on one side irregularly shallowly lobate-laciniate, on the other undivided and broadly rounded; bracteole narrowly to broadly united with one of the bracts, lanceolate to linear, at times as long as the bracts. Perianth elongate-ovate, the upper 0.5 or more of the perianth deeply plicate and twisted, the perianth contracted to the somewhat truncate mouth; mouth shallowly and bluntly lobulate, entire to weakly crenulate, the marginal cells short-rectangular to moderately long-rectangular, with evenly thickened walls without trigones; perianth 2–3-stratose in basal portion.

Capsule ellipsoidal, the wall about 55–65 μm thick, 5–6-stratose; outer layer of cells with radial longitudinal walls thin-walled, with nodular to short spur-like thickenings primarily on alternating radial walls; innermost layer of cells irregular in shape, the radial longitudinal walls with discontinuous sheets of wall material, mostly with nodular to spine-like thickenings, only sporadically with complete semiannular bands.

Spores 15.4–17.3 μm in diam., finely and closely papillose. Elaters bispiral to tips, 7.2–8.6 μm wide.

Distribution and Ecology: Endemic to New Zealand: South Island (ca. 150–1010 m), North Island (30–540 m), Chatham Islands (80–240 m). Known from Western Nelson (Stockton Plateau, Punakaiki), Southern North Island (Eastbourne), Volcanic Plateau (Rotorua), Gisborne (Mahia Peninsula), Auckland and Northland EPs. Most common in the northern half of the North Island, but the highest recorded elevation is from the summit of Mt. Augustus (Stockton Plateau, 1010 m).

The species has a sporadic distribution and typically occurs over clayey soil of banks. For example, it occurs over a wet, silty roadside bank draining a pakihi (1 km N of White Horse Creek, near Punakaiki, ca. 150 m) or on a roadside bank with *Blechnum* beneath *Agathis* forest (N of bridge on State Highway 12 over Waipoua River, Northland, 110 m). At Takapuna (Auckland) it has been collected on coastal cliffs. Also on granitic roadside banks covered

mostly by hepatics, mosses, *Blechnum* and *Stereocaulon* (N side of Tiropahi River, 145 m). Also found on a vertical, moist, shaded bank in a scrub forest of *Leptospermum scoparium*, *Weinmannia silvicola* and *Dacrydium cupressinum* (ridge between Webb Creek Track and Billy Goat Track, Coromandel Forest Park, 510–540 m). In the Rotorua area it has been found on thermal ground with *Campylopus clavatus*. Other associated species are *Cladia aggregata*, *Fissidens tenellus* var. *tenellus*, *Herzogianthus vaginatus* (on Rainbow Mtn., Rotorua) and *Jamesoniella colorata*.

Comments: This species is clearly distinct from related New Zealand species by the broadly overlapping dorsal leaf bases, with leaf insertions extending across and well beyond the dorsal stem midline (Fig. 161: 1). This condition lends a zigzag appearance to the leaf bases in dorsal aspect (Fig. 161: 1). However, ♂ bracts of *Cryptochila grandiflora* also have this zigzag appearance and the presence of trigones should be used to confirm the species. The species otherwise bears a superficial resemblance to *Jamesoniella colorata*, but lacks the coarse, guttulate papillae of that species. In addition, the dorsal margin of the leaves is not decurrent (Fig. 161: 1) as in other New Zealand species of *Jamesoniella* and *Cryptochila*.

Cryptochila grandiflora (Lindenb. & Gottsche) Grolle

[Fig. 158: 4, 5, oil-bodies, p. 724; Fig. 162]

Jungermannia grandiflora Lindenb. & Gottsche *in* Gottsche, Lindenb. & Nees, Syn. Hepat. 673. 1847. *Jamesoniella grandiflora* (Lindenb. & Gottsche) Jack & Steph., Hedwigia 31: 13. 1892. *Cryptochila grandiflora* (Lindenb. & Gottsche) Grolle, Feddes Repert. 82: 19. 1971. Type: Chile, Valdivia, *Gay*.

Jamesoniella sonderi Steph., Hedwigia 34: 48. 1895. Type: Tasmania, (Mt. Wellington, 1350 m), *Moore 48*.

Jungermannia sonderi Gottsche, Linnaea 28: 550. 1856. *Jamesoniella sonderi* (Gottsche) Steph., Sp. Hepat. 2: 99. 1901, *non Jamesoniella sonderi* Steph., 1895 = *C. grandiflora*. Lectotype (*fide* Grolle, 1971a): Australia, Australian Alps, *F. von Mueller* (L, *non vidi*).

Jamesoniella hectorii Berggr., New Zealand Hepat. 15. *f. 11*. 1898. Lectotype (*fide* Grolle, 1971a): New Zealand, South Is., "in alpibus ad flumen Bealey," *Berggren 2843* (LD, *non vidi*).

Jamesoniella nervosa Berggr., New Zealand Hepat. 13. *f. 10*. 1898. Lectotype (*fide* Grolle, 1971a): New Zealand, South Is., "in alpibus ad flumen Bealey," *Berggren 2839* (LD, *non vidi*).

Plants ascending, in deep, loose tufts, arising from underlying shoots with decomposed leaves (or in drier situations the plants procumbent on soil and adhering by stolons), often green, deep reddish brown to deep magenta (but never pure reddish), becoming blackish in exposed sites, the plants to 1.5 mm wide. Stems wiry, often reddish brown to blackish, the cortex moderately sharply differentiated, the epidermal layer of cells evenly thick-walled, the 2–3 subepidermal layers with moderately thickened and often deeply pigmented walls; medullary cells thin-walled, colorless. Rhizoids mostly confined to stolons, but at times also on the ventral side of prostrate normal leafy shoots. Branching exclusively ventral-intercalary, in sterile shoots mostly confined to basal portion of plant. Leaves vertically oriented when dry, concave, appressed to stem, ventrally secund, when moist obliquely divergent, subsquarrose, the basal portion sheathing the stem (in suboptimal forms the leaves plane and distinctly dorsally assurgent), the insertion weakly succubous to almost transverse, not crossing the stem midline dorsally, leaves broadly elliptic to orbicular to oblate, 1000–3000 μm wide × 930–2250 μm long, entire, the apex broadly rounded, strongly contracted to the base; dorsal margin typically

erect-inflexed to distinctly involute (particularly when dry), moderately to distinctly arched, long-decurrent at base; ventral margin moderately to strongly ampliate, contracted to the base, short-decurrent; paraphyllia absent or present on dorsal side of stem between the leaves, inconspicuous, needle-like. Cells in concentrically radiating rows (especially evident in distal sector of leaves), quadrate to short-rectangular, moderately to very strongly and evenly thick-walled, particularly toward the distal margins; trigones lacking or very small and indistinct; cells of upper median portion of leaf 15–21 × 18–26 μm; median-basal cells elongated, in a distinct vitta-like field, uniformly thickened or with knob-like thickenings of the longitudinal walls; surface typically finely, delicately, rather distantly and indistinctly striolate-papillose lending a "speckled" appearance, occasionally smooth, the median-basal cells striate-papillose. Oil-bodies occupying moderate portion of cell lumen, very pale smokey grey, 2–8(10) per median leaf cell, finely to coarsely papillose, the spherules not protruding beyond membrane, the oil-bodies globose to subglobose to broadly elliptic, often somewhat irregularly so, 2.9–4.3 × 4.3–5.8 μm to 4.8–5.8 × 8.2–9.6 μm, spherical ones 3.4–3.8 μm to 5.8–8.2 μm in diam. Chloroplasts large for cell and oil-body size. Underleaves absent or vestigial, caducous, uniseriate, filamentous; ventral merophyte very narrow, forming a continuous, pale, median-ventral strip.

Androecia on leading shoots, of similar width to vegetative sectors or slightly narrower, with up to 7 pairs of bracts; bracts saccate in basal portion, the dorsal margin strongly and narrowly involute, the free margin somewhat dilated and inflexed, broadly rounded, entire or rarely with a weak tooth; antheridia solitary, the stalk biseriate. Gynoecia usually not innovating; subinvolucral leaves gradually becoming somewhat larger, the innermost bracts somewhat smaller, free from one another, mostly broadly obovate, on one side coarsely toothed to lobulate-lobate-laciniate, the opposing bract undivided and broadly rounded at apex or 2–3-lobed to ca. 0.3, the lobes broadly rounded; bracteole united up to 0.3 its length with one or both bracts, very narrowly lanceolate, almost as long as the bracts, with 1–2 broad-based teeth on one or both margins; bract and bracteole bases sometimes with lanceolate accessory lamellae. Perianth elliptic, plicate in upper 0.5 or sometimes nearly to base, the distal portion twisted, the perianth contracted to the somewhat truncate mouth; mouth shallowly and bluntly lobulate, almost entire or weakly crenulate, the marginal cells subquadrate, with uniformly thickened walls without trigones; perianth 3-stratose toward base.

Capsule ovoid-ellipsoidal, the wall 71–78 μm thick, 5–7-stratose; outer layer of cells irregular in shape, the longitudinal walls with strong, nodular thickenings that sometimes extend as short spine-like projections onto outer wall; innermost layer of cells irregular in shape, with semiannular bands closely spaced, normally complete, sporadically forked.

Spores 16.8–19.2 μm in diam., papillose, the papillae often forming short non-anastomosing vermiculate ridges. Elaters bispiral, 7.5–9.6 μm wide.

Distribution and Ecology: Pan-south-temperate in distribution. New Zealand: Campbell Island, Stewart Island (5–690 m), South Island (120–1370 m), North Island (670–1700 m); Australia: Macquarie Island, Tasmania, southeast Australia; New Guinea (4400–4600 m); South Sandwich Islands; South Georgia; Falkland Islands; southern South America; Andes north to Guatemala; Brazil (Serra do Itatiaia); Tristan da Cunha; Gough Island; Africa from Cape of Good Hope to Natal (3153 m); Marion Island; Prince Edward Island; Crozet Island; Kerguelen Island. In New Zealand known from Fiordland, Southland, Otago, Westland, Canterbury (near the Main Divide), Western Nelson, Sounds–Nelson (Richmond Ra.), Southern North Island (Tararua Ra.), Volcanic Plateau (Kaimanawa Ra., Mt. Ruapehu), Taranaki (Mt. Taranaki), Gisborne (Hikurangi) and Auckland (Great Barrier Island, Coromandel Peninsula) EPs.

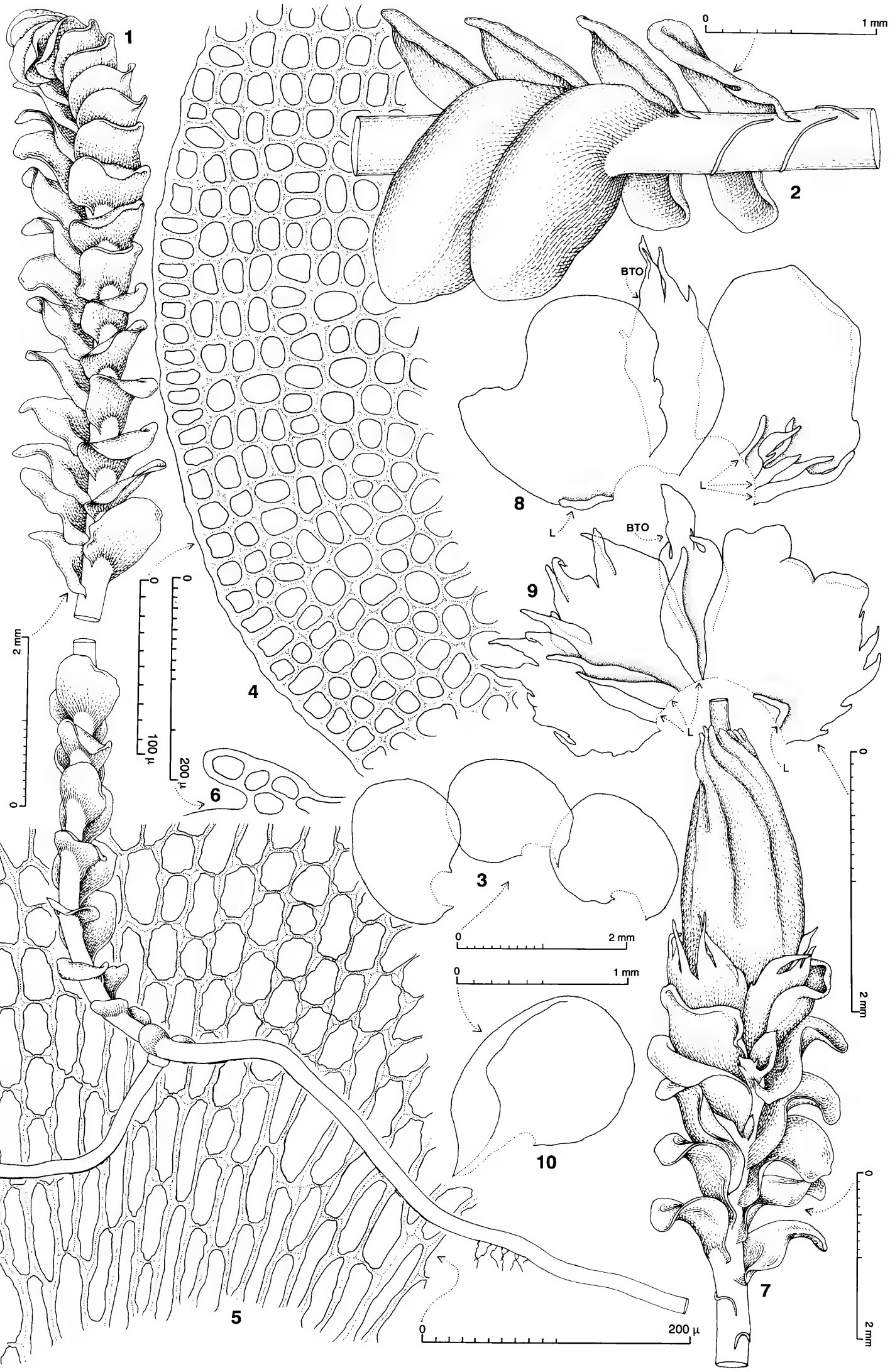

Fig. 162.
Cryptochila grandiflora (Lindenb. & Gottsche) Grolle. 1. Shoot with recurved shoot tip, basal stoloniform axis and ventral-intercalary stoloniform branch, ventral-lateral view. 2. Sector of main

The species typically occurs at elevations above 700 m on both South and North islands. It occurs in wet *Nothofagus* forests, where it may be found on cliff faces, large rock outcrops and bryophyte-covered boulders, but particularly along watercourses on soil over boulders. In the penalpine zone it is found in streams under scrub, e.g., of *Brachyglottis rotundifolia* and *Halocarpus biformis*. Also at lower elevations, e.g., on top of a boulder in a streambed in an *Agathis australis* forest with *Weinmannia silvicola* in a steep-sided stream valley (Waikohatu Stream at Waikohatu Kauri Bridge, Waipoua Forest, Northland, 290 m). Also found on a periodically inundated boulder at the margin of a stream under a canopy of *Melicytus ramiflorus* and *Cyathea dealbata*, and occasional dense pockets of *Freycinetia baueriana* in an otherwise open forest canopy of *Beilschmiedia tawa* and *Weinmannia silvicola* (headwaters of Poupou Stream, Kaimai-Mamaku Forest Park, Kaimai Ra., 400–425 m). In the alpine zone it can be found on rocks on tarn and pool margins, in streamlets in *Chionochloa* tussockland, and at higher altitudes in seepage from late-melting snowbanks. On Stewart Island occurring submerged on rock immediately above Belltopper Falls in an open, humid niche dominated by bedrock with a forest margin of *Weinmannia racemosa* and *Dracophyllum* (Port Pegasus, ca. 5 m). On Stewart Island also under considerably drier conditions, e.g., on a sandy exposed bank at 5 m in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium* – *Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus* (track to Mason Bay, ca. 1–1.8 km W of Freshwater Landing). In the penalpine and alpine zones, the species occurs on dripping rock faces and along watercourses over soil-covered rocks and boulders, on silty banks and in waterfall splash zones, etc., sometimes forming large pure stands. It is tolerant of periodic inundation in rivulets, and in such situations the species may become abundant. At the summit of Mt. Rakeahua (Stewart Island, 600–690 m) the species was found in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* 0.5–2 m tall and significant areas of exposed rock. It has been found with *Allisoniella nigra*, *Blindia immersa*, *Campylopus clavatus*, *Chiloscyphus austrigenus*, *Ditrichum strictum*, *Hepatostolonophora rotata* var. *rotata*, *Isotachis lyallii*, *I. montana*, *Nothogymnomitrion erosum*, *Pachyglossa tenacifolia*, *Racomitrium crispulum*, *Rhacocarpus purpurascens*, *Riccardia crassa* and *Triandrophyllum subtrifidum*.

Comments: This species is most easily recognized by its markedly squarrose leaves, particularly when moist. The superficial aspect of the plants is sometimes strikingly like that of *Cryptochila pseudocclusa*, but unlike that species the dorsal leaf margin is erect-inflexed to involute (Fig. 162: 1, 2), rather than narrowly and tightly revolute. Both species have ventrally secund leaves with strongly ampliate ventral margins, the asymmetry of the leaves accentuated *in situ* by the strong curvature of the dorsal margins.

In the absence of gametangia, *Cryptochila grandiflora* can easily be mistaken for *Adelanthus occlusus* (p. 625), an erect plant of similar stature with vertically oriented, entire leaves (Fig. 134: 1, 3). The similarity extends to the concentrically radially aligned arrangement of the leaf cells, the apparent absence of underleaves, the presence of basal microphyllous stoloni-

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shoot, lateral view. 3. Leaves. 4. Cells of leaf apex. 5. Median-basal leaf cells. 6. Stem paraphyllium (*in situ*, lateral aspect). 7. Gynoecium with mature sporophyte, ventral view. 8, 9. Innermost ♀ bracts and, in middle, bracteole (= BTO; L = accessory lamellae; both at same scale). 10. ♂ Bract. (Figs. 1–9, from *Hatcher 295a*, New Zealand, North Is., Taranaki EP, Pukeiti Bush; 10, from *Hatcher 1743*, New Zealand, South Is., Fiordland EP, head of Lake McKerrow.)

form branches, and the uniformly thick-walled leaf cells. In general, however, the leaves of *A. occlusus* are almost flat and never squarrose, and the tips of leafy shoots bear 2-celled, ellipsoidal, green gemmae. In addition, *Adelanthus* bears gametangia on strongly reduced intercalary branches, all or mostly from leafless lower sectors of the main shoot or from stolons (Fig. 132: 1; Fig. 133: 1, 2); these can usually be found with careful search.

Smaller, less markedly squarrose, orbicular-leaved expressions of the species superficially resemble *Jamesoniella colorata* (p. 722), but can be distinguished by the smooth surface and the evenly thick-walled leaf cells, lacking trigones (Fig. 162: 4). In addition, *J. colorata* is typically reddish tinged to deep wine-red in color, whereas *Cryptochila grandiflora* is a warm golden brown to reddish brown. The two species may be distinguished by the following couplet.

1a. Leaf surface smooth; trigones lacking; stem cortex in 3(4) cell layers with strongly thickened walls; perianth strongly spirally twisted distally; innermost bracts differentiated from one another: one undivided, the other dentate to lobulate; bracteole markedly narrowly connate to 1 of adjacent bracts, narrowly lanceolate . . . . . *Cryptochila grandiflora*

1b. Leaf surface coarsely papillose; trigones medium to bulging; stem cortex poorly differentiated, in 1 layer of thickened cells; perianth not twisted distally; innermost bracts not differentiated from one another, of similar size and form, deeply dissected by copious, irregular, mostly lanceolate processes; bracteole very broadly connate to 1 of adjacent bracts, irregularly laciniate-lobulate . . . . . *Jamesoniella colorata*

The genus *Hepatostolonophora* superficially resembles *Cryptochila grandiflora*, and also is frequently found growing in sites along penalpine–alpine streamlets. The plants are usually softer and laxer than those of *C. grandiflora*, it never has red or brown pigments and the leaves are more distant, flaccid and contorted when dry. *Hepatostolonophora* can always be distinguished by the presence of the highly characteristic, very narrow, deeply dissected underleaves, although these are colorless and appressed to the stem and are easily overlooked.

Cryptochila pseudocclusa (E.A.Hodgs.) R.M.Schust.

[Plate 14C–E; Fig. 158: 6, oil-bodies, p. 724]

Jamesoniella pseudocclusa E.A.Hodgs., Trans. Roy. Soc. New Zealand 73: 79. 1946, *nom. nud.* (*sin. descr. lat.*), Trans. Roy. Soc. New Zealand 85: 583. 1958. *Cryptochila pseudocclusa* (E.A.Hodgs.) R.M.Schust., J. Hattori Bot. Lab. 26: 284. 1963. Holotype: New Zealand, North Is., near Ohakune Mtn. Hut, 4500 ft., Dec. 1929, *Sainsbury* (herb. Hodgson no. 126) (MPN, *non vidi*).

Plants ascending to erect, vigorous, brownish green to brownish, to 6(10) cm high, to 2 mm wide (in lateral aspect). Stems rigid, light green or whitish above, becoming blackish, the cortex sharply differentiated, the epidermal 1(2) layers of somewhat lighter and thinner-walled cells, the 2–3 subepidermal layers with thickened and strongly pigmented walls; medullary cells thin-walled, colorless. Paraphyllia scattered, delicate, on both dorsal and ventral surfaces of stem. Rhizoids rare, only from stolons, rarely from leafy stems. Branching sparing (shoots often unbranched), ventral-intercalary, also terminal, *Frullania* type; geotropic, narrow and whip-like, flagelliform branches produced from the lower portions of leafy shoots or from just above branch bases. Leaves densely imbricate, nearly vertical, erect-appressed (especially when dry), the shoots bilaterally compressed, very strongly ventrally secund, appearing incubously shingled in dorsal aspect, the insertion steeply oblique in dorsal portion, becoming subtransverse, abruptly recurved at ventral end, the dorsal leaf bases closely juxtaposed but not crossing stem midline; leaves strongly asymmetric, reniform, entire, 1450–1750 μm wide

× 1400–2000 μm long, the apex broadly rounded; dorsal margin tightly and narrowly revolute for most of its length, strongly arched, distinctly and narrowly decurrent at base; ventral margin nearly plane, extraordinarily ampliate, short-decurrent. Cells in concentrically radiating rows, the cells in distal and marginal sectors of leaf quadrate to short-rectangular, evenly thick-walled, the cells in median portion of leaf with small to medium and straight-sided to bulging trigones; cells of upper median portion of leaf 17–23 μm wide × (18)20–26 μm long; median-basal cells distinctly elongated, forming a moderately large and strongly delimited basal area, the cells with bulging to knot-like and subconfluent trigones and intermediate thickenings of the longitudinal walls; surface smooth, long-striate toward the leaf base. Oil-bodies occupying a moderate portion of the cell, hyaline, but with a milky appearance, 8–12 per median leaf cell, irregularly and coarsely papillose, the spherules ill-defined and rapidly swelling and coalescing. Chloroplasts conspicuous for cell size. Oil-bodies (Schuster, 1970b) usually (5)6–11(12) per median cell, chiefly very finely granular to almost homogeneous but not glistening, with age developing 1–2 centric or eccentric "eyes," or somewhat botryoidal, variable, rather small, in median cells 2.5–3 × 2.8–6 μm up to 3–3.5 × 6–8 μm, ovoid or ellipsoidal to subspherical; marginal and submarginal cells often without oil-bodies. Underleaves deciduous, irregularly and palmately divided almost to base into 3–4 lobules each terminating in an elongate slime papilla, the ventral merophyte narrow, forming a continuous, pale, median-ventral strip. Gemmae lacking.

Androecia on leading shoots, somewhat wider than vegetative sector (dorsal view), with 5–8 or more pairs of bracts; bracts resembling leaves but with a deep basal concavity, the dorsal base dilated and sharply reflexed, the margin narrowly revolute; lobule an inconspicuous, irregular, low lamelliform strip; antheridia single, the stalk biseriate. Gynoecia not innovating, at apices of main shoots; subinvolucral leaves somewhat larger, the bracts of innermost series a little smaller, variable, incised-lobulate to laciniate, the apex and margins crispate; bracteole variable, ovate, incised-lobate, the margins coarsely toothed to laciniate. Perianth cylindrical but gradually tapered distally, strongly and deeply pluriplicate in upper 0.5–0.65, the plicae at times extending nearly to the base, the distal 0.4–0.75 of the perianth strongly twisted, the perianth somewhat contracted toward the mouth; mouth shallowly lobulate and weakly crenulate, the marginal cells quadrate to short-rectangular, with weakly thickened walls lacking trigones.

Capsule intense red, ellipsoidal to ovoid, the wall 6–7-stratose, ca. 60 μm thick; outer layer of cells irregular in shape, with longitudinal and all but very short transverse walls with strong, nodular thickenings commonly extending as spine-like projections onto outer wall; innermost layer of cells very irregular in shape, with complete or less often incomplete semiannular bands.

Spores 14–20.6 μm in diam., finely papillose, the papillae often forming short-vermiculate ridges. Elaters bispiral, the spirals distinct to the rather blunt ends, 7.5–8.5(10) μm wide.

Distribution and Ecology: Endemic to New Zealand: Auckland Islands (300 m), Stewart Island (5–400 m), South Island (600–1900 m), North Island (1280–1650 m). Known from Fiordland, Otago (Mt. Cargill), Westland, Canterbury (near the Main Divide), Western Nelson, Southern North Island (Tararua Ra.) and Volcanic Plateau (Mt. Ruapehu) EPs.

For the most part a middle- to upper-elevation species. In wet, rich *Nothofagus menziesii* forests the species may occur, for example, on thick soil over rock faces (summit area of Haast Pass, Mt. Aspiring Natl. Park), including road banks with seepage. In the penalpine and alpine zones it occurs on soil at the lips of rills or at the edge of boulders (Gertrude Valley, off track to Gertrude Saddle, Fiordland Natl. Park, 1880–1900 m). At Round Lake (Cobb Valley, Western Nelson, 1300 m) it was on sandstone in a steep stream in *Chionochloa rubra*, *Schoenus*

pauciflorus and *Bulbinella hookeri* sedgeland, growing with *Anisotome aromatica*, *Forstera tenella* and *Ourisia lactea*. However, along the track to Bowen Falls (Milford Sound, Fiordland Natl. Park) the species occurs at sea level on vertical cliffs with dense bryophyte cover. On Stewart Island near sea level (5 m) on sandy soil in mosaic communities of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium – Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma minus*. In Westland it is found in penalpine gullies under *Olearia colensoi* scrub. It is found with *Anastrophyllum schismoides*, *Andreaea acuminata*, *Breutelia pendula*, *B. elongata*, *Chiloscyphus leucophyllus*, *Conostomum pentastichum*, *Herzogobryum teres*, *Hymenophyllum armstrongii*, *Isotachis lyallii*, *I. montana*, *Lepidozia obtusiloba*, *Paraschistochila conchophylla*, *Racomitrium crispulum*, *R. pruinosum*, *Radula sainsburiana*, *Rhacocarpus purpurascens*, *Sphagnum falcatulum* and *Wijkia extenuata*.

Comments: This species stands apart from all others in the genus by the narrowly and tightly revolute dorsal margins of the leaves, a feature that may be easily observed in the field. The habitus of the plant is, however, strikingly similar to certain *Plagiochila* species, namely *P. circinalis*, which also has erect-appressed, entire-margined, broadly rounded leaves with a strongly revolute dorsal margin. The shoots of *P. circinalis*, however, lack stem paraphyllia, and the leaf cells have coarsely nodulose trigones. *Cryptochila grandiflora* may be distinguished, even in the field, by the inflexed dorsal leaf margins.

Cryptochila acinacifolia (Hook.f. & Taylor) Grolle

[Fig. 163]

Jungermannia acinacifolia Hook.f. & Taylor, London J. Bot. 3: 367. 1844. *Gymnomitrium acinacifolium* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 616. 1846. *Acolea acinacifolia* (Hook.f. & Taylor) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 395. 1877. *Cesiusa acinacifolia* (Hook.f. & Taylor) Kuntze, Revis. Gen. Pl. 2: 833. 1891. *Jamesoniella acinacifolia* (Hook.f. & Taylor) Berggr., New Zealand Hepat. 14. 1898. *Cryptochila acinacifolia* (Hook.f. & Taylor) Grolle, Feddes Repert. 82: 29. 1971. Lectotype (*fide* Grolle, 1971a): Campbell Is., *Hooker* (BM, *non vidi*).

Plants rigid, loosely prostrate, the shoot apex slightly curved upward, the plants as semi-scattered shoots or in very compact tufts and then with a densely interwoven mat of leafless, stoloniform branches beneath, the plants deep reddish brown to blackish, the shoots to 2 cm long, to 1.6 mm wide. Stems light to deep brown, the cortical cells not sharply delimited, in 2–4 layers of darker-pigmented, evenly thick-walled cells; medullary cells somewhat larger, pale, unevenly thick-walled. Paraphyllia lacking in sterile shoot sectors. Rhizoids on stolons and the lower portions of normal leafy shoots. Branching always ventral-intercalary, in sterile portions of the shoot from basal or distal sectors of shoot; leafless, geotropic stoloniform branches abundantly produced, often arising near the base of leafy branches. Leaves multistratose in basal portion, the multistratose portion broadest at insertion, extending from dorsal margin to the vitta (to ca. 15 cells wide), narrowing distally, the leaves rigid, densely imbricate, the leaves when dry dorsally obliquely assurgent and laterally appressed to stem, when moist the distal portion obliquely to widely spreading, the ventral leaf bases tightly shingled and appressed to stem, the dorsal margins plane, not undulate, stiffly vertically oriented from base to tip (seen on edge in dorsal view), the median base concave, the insertion weakly succubous to nearly transverse, not crossing the stem midline dorsally, the leaves narrowly elliptic to oblong, to 2:1, lingulate, 410–440 μm wide × 750–820 μm long, the apex rounded; dorsal

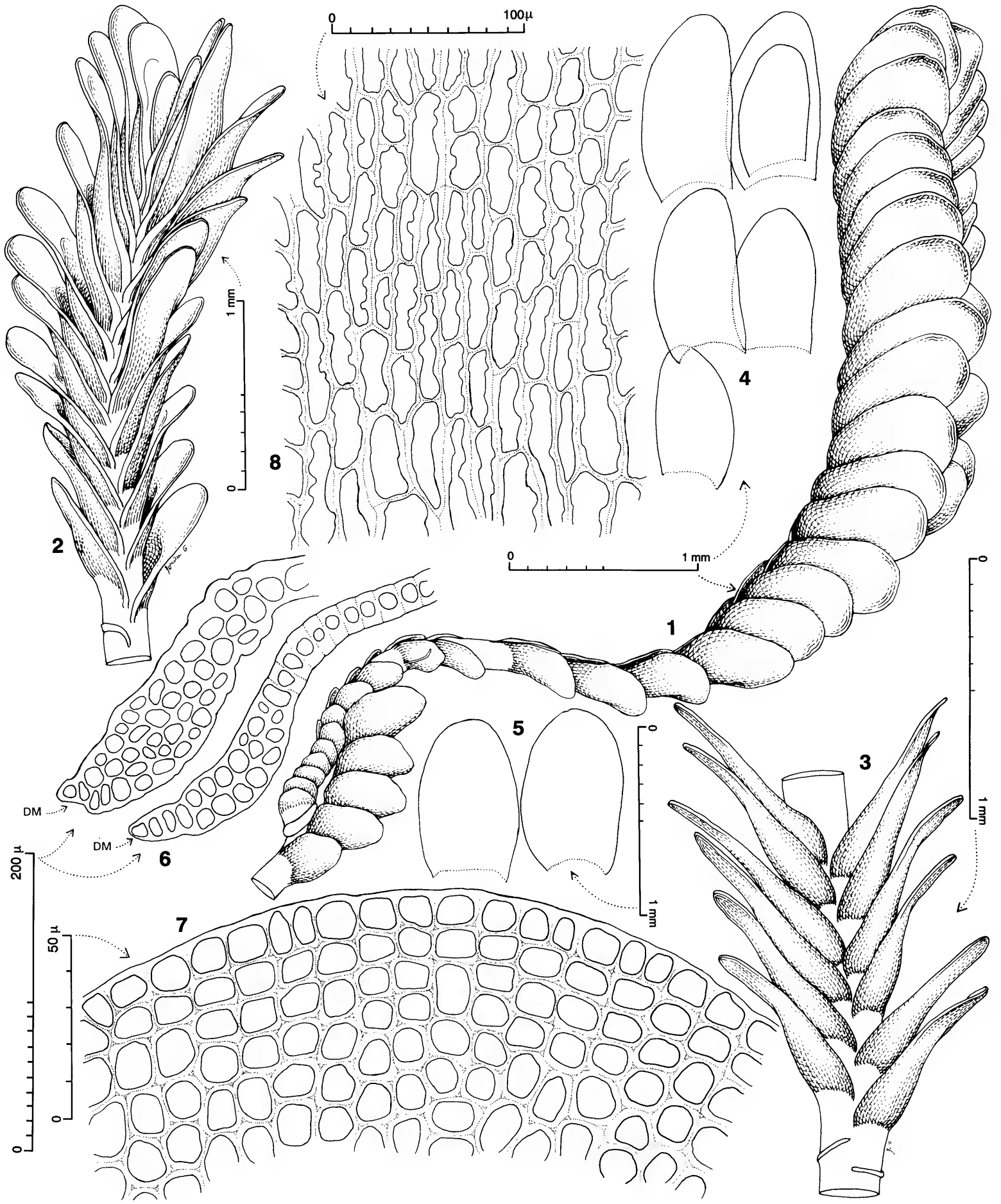

Fig. 163.
Cryptochila acinacifolia (Hook.f. & Taylor) Grolle. 1. Lower sector of older, leading shoot with an erect, leafy ventral-intercalary branch, lateral view. 2. Portion of leading leafy branch, dorsal view. 3. Portion of leading leafy branch, ventral view. 4, 5. Leaves. 6. Leaf, cross sections through base (DM = dorsal margin). 7. Distal sector of leaf. 8. Median-basal leaf cells. (Figs. 1–4, 6–8, from *Vitt 2402B*, Campbell Is.; 5, from *Child H4597*, New Zealand, South Is., Westland EP, Kelly's Hill, N of Otira.)

margin almost straight, thickened and 2–3(4)-stratose in and some distance above the moderately decurrent base (at times in lower 0.5 of leaf); ventral margin weakly arched, especially at the base, not or very short-decurrent. Cells in distal portion with uniformly strongly thickened walls, the cells toward the leaf apex and margins subquadrate, isodiametric, 11–14 μm wide and long, the marginal cells at times bleached, but not thicker-walled; median-basal cells elongated (to 5.6:1), forming a broad vitta-like sector occupying the middle third of leaf, the cells evenly thick-walled or with knob-like thickenings on longitudinal walls; surface smooth. Underleaves absent.

Androecia with up to 6 pairs of bracts; bracts pouched, with a small, thick, inflexed lobulus; antheridia single, the stalk biseriate. Gynoecia on leading shoots. Perianth (only young seen) broad-elliptic, contracted to mouth, deeply plicate nearly to base, the mouth shallowly lobulate, weakly crenulate, the marginal cells slightly elongated, the marginal and submarginal cells thick-walled.

Sporophytes unknown.

Distribution and Ecology: Endemic to New Zealand: Campbell Island (396–540 m), Stewart Island (530–1000 m), South Island (1000–1280 m). In the South Island known from Fiordland (Secretary Island, Mt. Alexander, Eldrig Peak), Westland (Kelly Ra., Westland, ca. 1400 m, *Child H4597*; *leg. Berggren* [Grolle, 1971a]) and Western Nelson (Mt. Euclid, Glasgow Ra.) EPs.

At the summit of Mt. Rocky (Stewart Island, 530 m) it occurred on south-facing, very exposed, prominent rocky outcrops, with a wind-pruned heath dominated by *Leptospermum scoparium* to ca. 50 cm high. At the summit of Mt. Rakeahua (also Stewart Island, 600–690 m) it was found on a thin layer of soil in a protected pocket at the base of a rock outcrop in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *L. scoparium* and *Olearia colensoi* from 0.5 m to 2 m tall and significant areas of exposed rock. On the Glasgow Ra. and Mt. Euclid it was found in soil pockets on shaded granite bluffs with *Schoenus pauciflorus*, *Grammitis poeppigiana*, *Forstera sedifolia*, *Rhacocarpus purpurascens* and *Paraschistochila conchophylla*. Other species that have been found with *Cryptochila acinacifolia* are *Andreaea mutabilis*, *Andrewsianthus cuspidatus*, *Campylopus clavatus*, *Conostomum pentastichum*, *Hepatostolonophora rotata*, *Herzogobryum teres*, *Jamesoniella colorata*, *Racomitrium crispulum*, *Radula sainsburiana* and *Wijkia extenuata*.

Comments: This rare species has lingulate leaves like those of *Jamesoniella kirkii* (p. 717), but lacks the distinctive transversely undulate dorsal margins and strongly developed knot-like trigones of that species. Its most unusual feature is the thickened, multistratose strip along the dorsal leaf margin near the insertion (Fig. 163: 6), clearly visible in dorsal aspect as a narrow, V-shaped wedge (Fig. 163: 2). The leaf cells of *Cryptochila acinacifolia* have uniformly thickened walls, as in *C. grandiflora*.

Family **SCAPANIACEAE** Mig.

Scapaniaceae Mig., Krypt.-Fl. Deutschland 1: 479. 1904.

Plants procumbent (rarely closely creeping) to erect, especially with crowding, in direct light developing brownish or reddish or purplish pigments, small to vigorous, the shoots to 8 mm wide, the shoot tips autonomously arched away from substrate. Branching sparing, irreg-

ular, remote, the branches nearly always lateral-intercalary, lateral in position in leaf axils but at times at ventral end of axil (then simulating ventral-intercalary branches); ventral-intercalary branches present in *Diplophyllum* subg. *Macrodiplophyllum* and *D. recurvifolium*; *Frullania*-type branches sometimes present in *Scapania* subg. *Jensenia*; basiscopic, *Radula*-type branches present in a few taxa. Stems often mycorrhizal with age, the cortex ± well differentiated, in (1)2–4(5) layers of thick-walled, often smaller, usually pigmented cells. Rhizoids usually frequent, scattered. Leaves basically vertically oriented, complicate-bilobed, usually strongly folded and with the lobes connected by a keel, the keel sharp or, less often, blunt, frequently ridged or winged, the ventral lobe slightly to more often distinctly larger (the lobes exceptionally subequal), the insertion extended to stem midline but not beyond, basically with the dorsal half at least in part (and often largely) transverse, but with ventral half oblique and succubous (mechanically thus ensuring that the dorsal lobe lies over the ventral); lobe apices rounded-apiculate, the lobe margins usually variously, often copiously dentate to ciliate, sometimes entire, the free margin of the dorsal lobe often decurrent, the decurrent strips running down stem midline. Cells ± collenchymatous, medium-sized (rarely over 25–35 μm wide in lobe middle); surface usually clearly papillose. Oil-bodies (Schuster, 2002a) in all cells, usually (1)2–10 per cell, granular or granular-botryoidal. Underleaves lacking, even in gynoecium or associated with gemmae production; ventral merophytes maximally reduced, the ventral ends of leaf insertions impinging on stem midline. Asexual reproduction by gemmae, the gemmae almost universally present, 1–2(5)-celled, with strongly protuberant angles, formed in branched chains from margins of uppermost leaf lobes (the leaves usually little or unmodified).

Dioecious, less often autoecious or paroecious. Androecia on leading leafy shoots, terminal but with age becoming intercalary, the bracts leaf-like but bases ventricose, at times moderately smaller than leaves; antheridia (1)2–4(7) per bract, the stalk uniseriate (2-seriate in subg. *Austrodiplophyllum* spp.); paraphyses often present. Gynoecia on leading leafy shoots, the bracts leaf-like, marginally to moderately larger than leaves; bracteole lacking. Perianth conspicuous, elongated, without stem-derived components, dorsiventrally compressed (sporadically weakly so), the mouth wide or only weakly contracted, distally smooth and with two flat faces, but these sometimes plicate.

Seta strongly elongating, massive, of many rows of undifferentiated cells. Capsule ovoid-ellipsoidal (rarely almost spherical), the wall (3)4–6(7)-stratose; outer layer of cells with radial (I-shaped) thickenings on all longer and all but shortest transverse walls, the thickenings usually clearly separated; inner layer of cells with semiannular bands.

Spores mostly 11–20 μm in diam., papillose or with confluent papillae and then vermiculate, 1.3–3× elater diam. Elaters feebly tortuous, bispiral (1-spiral in *Douinia*), with weakly tapered ends.

Type: *Scapania* (Dumort.) Dumort.

A family chiefly of cool to cold to Arctic regions of the Northern Hemisphere. Grolle (1983) divided the family into four subfamilies and included seven genera. One of the genera, *Delavayella* Steph., a monotypic genus ranging from the Himalayas to Thailand, was placed in subfamily *Delavayelloideae* by Grolle (1966f, 1983), but is assigned to a separate family, the *Delavayellaceae* R.M.Schust. by Schuster (1961c, 1974a, 1999c, 2002a) and by Potemkin (1999). Grolle (1983) recognized subfamily *Blepharidophylloideae*, as did Schuster (1974a), but the group was placed at the family rank by Schuster (1974a, 1999c, 2002a), by Engel

(1990a), where the family name was validated, and by Potemkin (1999). *Krunodiplophyllum* Grolle (Grolle, 1965d) was placed in the synonymy of *Diplophyllum* subg. *Austrodiplophyllum* by Engel and Merrill (1998). Potemkin (1999) removed *Diplophyllum* and *Douinia* into the separate family *Diplophyllaceae*, and merged *Macrodiplophyllum* with *Scapania*. The *Scapaniaceae* eventually may become monogeneric if these taxonomic placements are accepted, especially with the inclusion of molecular studies.

We include three genera in the family. The two larger genera, *Scapania* and *Diplophyllum*, occur in our area; *Douinia* Buch is monotypic and found in Europe, western North America and Japan. Schuster (2002a, p. 460) remarks that the "few antipodal taxa…appear, probably, to be derived from Laurasian antecedents and the family is here regarded as of Laurasian origin."

Description of family after Schuster (2002a) but freely modified.

Diplophyllum (Dumort.) Dumort.

Diplophyllum (Dumort.) Dumort., Recueil Observ. Jungerm. 15. 1835; *nom. cons. Jungermannia* sect. *Diplophyllum* Dumort., Syll. Jungerm. Europ. 44. 1831.

Plants prostrate or erect, often in thin, flat patches, clear green or yellowish green (in shade) to yellowish brown, or reddish to reddish orange to reddish brown to blackish, small to medium-sized, to 4.5 mm wide. Branching sparing, the branches lateral-intercalary (rarely displaced to ventral angle of leaf); ventral-intercalary branches present in *Diplophyllum recurvifolium*. Stem with cortex in 1–2 layers (3–5 in *D. albicans* and subg. *Macrodiplophyllum*), of ± firm-walled cells; medullary cells larger, often mycorrhizal with age. Rhizoids scattered. Leaves usually lying in one plane, complicate bilobed, the two lobes usually widely divergent, at least ventral halves widely spreading (sometimes squarrose), the keel rounded or obtuse, never winged, the base ± sheathing. Ventral lobe narrowly lingulate, ± falcate, typically more than 2× longer than wide, distinctly decurrent at the base (subg. *Macrodiplophyllum*) or not decurrent. Dorsal lobe similar to the ventral but smaller and shorter (subequal to the ventral in subg. *Austrodiplophyllum*), mostly suberect or obliquely spreading (except *D. verrucosum*). Leaf lobes with apices rounded or blunt to apiculate (long-acuminate in *D. andicolum*), the apices and margins denticulate or serrulate by small, sharp teeth. Cells small, usually firm-walled, the median cells with trigones small or inconspicuous (except subg. *Macrodiplophyllum*); marginal cells in several rows, often strongly and equally thick-walled, isodiametric; basal cells of ventral lobe and keelar region elongate-rectangular (ca. 3–5× longer than wide and often forming a sharply delimited vitta); surface of median cells with dense, often large papillae, the papillae often inconspicuous or absent in marginal cells. Oil-bodies (Schuster, 1974a) distinctly segmented, papillose, usually 2–4(5) per intramarginal cell, 10–16 per elongated cell of basal, keelar region. Gemmae quadrate to polygonal-stellate, 1–2-celled (to 3–4-celled in subg. *Macrodiplophyllum*), with strongly thickened angles.

Dioecious, autoecious or paroecious. Androecial bracts leaf-like but with bases ventricose; antheridial stalks long, uniseriate or variably 1–2(3–4)-seriate. Gynoecial bracts leaf-like but ± larger, sheathing perianth at base only. Perianth weakly to moderately dorsiventrally compressed, especially above, elliptical in section below, distally deeply plicate, somewhat narrowed to the mouth, the mouth dentate to laciniate.

Capsule ellipsoidal, the wall 3–4-stratose; outer layer of cells with one-phase development, with nodular to spur-like thickenings (*Diplophyllum domesticum*) or at times locally with a

suggestion of a two-phase development: longitudinal walls with pigmented thickenings few or absent alternating with those with strong nodular to spur-like thickenings; inner layer of cells with nodular to often spur-like thickenings that occasionally tangentially extend to form incomplete to (less often) complete semiannular bands.

Spores 9–15 μm in diam., irregularly and finely papillose-vermiculate, the markings at times in part anastomose to form elevated, weak tubercles at the intersections, the spores at times with distinct, sharply defined, broad vermiculate markings. Elaters tortuous, 6–8 μm, bispiral.

Type (*cons.*): *Diplophyllum albicans* (L.) Dumort. (≡ *Jungermannia albicans* L.)

Diplophyllum is the second largest genus in the family, with 27 species worldwide, but has a greater representation in Austral areas than the largest genus, *Scapania*. Engel and Merrill (1998) recognized three subgenera, and of these, two occur in Austral areas.

1) subg. *Austrodiplophyllum* R.M.Schust. has four species, all Austral in distribution; *D. squarrosum* Steph. (Engel and Merrill, 1998; Grolle, 1965d) and *D. recurvifolium* C.Massal. (Massalongo, 1928; Engel and Merrill, 1998; Schuster, 1971b, 2002a) occur in southern South America. *Diplophyllum verrucosum* R.M.Schust. (Engel and Merrill, 1998; Schuster, 1968a, 2002a) and *D. gemmiparum* J.J.Engel & Merrill (Engel and Merrill, 1998) occur in our area.

2) subg. *Macrodiplophyllum* Buch has three species and is North Pacific; see Engel and Merrill (1998) for distribution of the species.

3) subg. *Diplophyllum* has nine Austral species. Interestingly, only one species, *D. acutilobum* Steph., occurs in southern South America (Engel, 1978) and the Falkland Islands (Engel, 1990a), contrasted to six species in Australasia. Of these, *D. novum* J.J.Engel & Merrill is endemic to New Zealand, *D. dioicum* R.M.Schust. occurs in New Zealand and Tasmania, *D. domesticum* (Gottsche) Steph. occurs in New Zealand, Tasmania, Victoria and New South Wales, and *D. androgynum* J.J.Engel & Merrill, *D. angustifolium* J.J.Engel & Merrill and *D. incrassatum* J.J.Engel & Merrill are endemic to Tasmania (see Engel and Merrill, 1998). *Diplophyllum marionense* S.W.Arnell is endemic to Marion Island (Arnell, 1953) [= *D. acutifolium fide* Arnell (1956, p. 529). "*D. randii* S. Arnell," mentioned by Schuster (1963b, p. 272) from Marion Island, was not listed by Grolle (1971a)]. *Diplophyllum africanum* S.W.Arnell occurs in Kenya (Mts. Elgon and Kilimanjaro, 3400–4200 m) (Arnell, 1956), Rwanda (Mt. Elgon and Kilimanjaro, 3650 m) (Váňa et al., 1979), and Tanzania (Bizot and Pócs, 1974).

Schuster (1974a, 2002a) included a fourth subgenus, subg. *Protodiplophyllum* R.M.Schust. (type = *Diplophyllum obtusifolium* (Hook.) Dumort.) and included 11 Austral and four Laurasian species (Schuster, 2002a). We would include this subgenus in the synonymy of subg. *Diplophyllum*.

Key to Species

1a. Leaves subequally bilobed, the dorsal lobe 0.7–0.9 the area of the ventral; leaf lobes (particularly the dorsal) distinctly squarrose-recurved. Subg. *Austrodiplophyllum* 2

2a. Plants ascending to (often) stiffly erect; rhizoids scattered; antheridial stalks 1- or 2-seriate or with some tiers 2-, 3- or even 4-seriate; gemmae rarely produced . . . . . *D. verrucosum* (p. 748)

2b. Plants loosely creeping to ascending; rhizoids in fascicles near ventral leaf bases (becoming scattered in older portions of shoot); antheridial stalks uniseriate; gemmae abundant, in terminal buds at apices of main shoot and branches . . . . . *D. gemmiparum* (p. 751)

1b. Leaves unequally bilobed, the dorsal lobe 0.25–0.5 the area of ventral (to 0.7 in *D. domesticum* var. *icari*); leaf lobes usually not squarrose-reflexed, the dorsal usually ± appressed to the ventral. Subg. *Diplophyllum* 3

3a. Ventral lobe with a distinct field of rectangular cells extending into distal half of lobe; plants often deeply reddish orange pigmented 4

4a. Dorsal and ventral lobe apices ± acute (especially the dorsal) and usually distinctly apiculate, the margin irregularly denticulate to serrulate; leaves ± transversely inserted in ventral half; plants typically small, to 1.4(1.6) mm wide. Plants consistently paroecious . . . . . *D. domesticum* (p. 757)

4b. Dorsal and ventral lobe apices broadly rounded to subtruncate, rarely minutely apiculate, the margin denticulate to subentire; leaves often obliquely inserted in the ventral half; plants larger, 1.8–2 mm wide. Plants paroecious, but androecia also on lateral-intercalary branches some distance below the terminal inflorescence. . . . . *D. novum* (p. 762)

3b. Ventral lobe with the distal half densely areolate, the cells in distal half uniformly isodiametric; plant green to yellowish brown, but never red. Vitta ± confined to keelar region; dioecious and typically sterile . . . . . *D. dioicum* (p. 754)

Diplophyllum verrucosum R.M.Schust.

[Plate 15C, D; Fig. 164]

Diplophyllum verrucosum R.M.Schust., Bull. Natl. Sci. Mus. Tokyo 11: 19. 1968. Holotype: New Zealand, South Is., Fiordland Natl. Park, between Lake Mackenzie and Harris Saddle, Humboldt Mtns., ca. 3800 ft., *Schuster 67-361* (F!).

Plants ascending to (often) stiffly erect, in shade clear green but with basal sheathing portion of leaves usually reddish pigmented, with exposure reddish orange with sheath a deep wine-red; shoots to 1.8(2.7) mm wide. Branches rather common and from leading leafy shoot to at times sparse and restricted to old, partially decayed, basal sectors, lateral-intercalary. Rhizoids not seen. Leaves rigid, brittle, stiffly spreading, weakly imbricate, conduplicate-bilobed, the base hollowed out and loosely sheathing the stem, the keel 0.4–0.6 the length of ventral lobe, rounded in section and not sharp, strongly arched, the cells forming the keel with exceptionally thick walls, the sinus acute and not or only weakly reflexed; dorsal and ventral lobes often subequal in size, widely divergent and ± regularly and symmetrically broadly squarrose-reflexed to distinctly falcate (the lobed tips directed inward toward the shoot), the shoots appearing 4-ranked, or the shoots plano-convex (in ventral view), the ventral lobe spreading at 90° or more from the stem but not or scarcely recurved; opposing dorsal leaf bases (when leaves imbricate) overlapping, extending to more than half the width of the stem; ventral bases distinctly overlapping, hiding the stem and extending across the full width of the stem. Ventral lobe orientation variable: broadly reflexed to plane to broadly inflexed, the in-

sertion of ventral half of leaf ± transverse, the free margin not decurrent, the lobe (when flattened) narrowly ovate to elliptic, often subfalcate; apex acute to broadly acute or at times somewhat blunted and apiculate, the apex denticulate, the tip often with a sharp, 1(2)-celled apiculus; ventral margin broadly arched, cordate at the base, the margins variable: usually rather finely and somewhat irregularly denticulate to the base, the teeth ± similar in size throughout, but in some populations the margin almost entire; dorsal margin often ± straight, toothed like the ventral margin or at times subentire; margins and apex with 1–several rows of cells often bleached white and eventually eroded away leaving an erose margin, particularly in exposed situations. Dorsal lobe broadly squarrose-reflexed, similar to the ventral in shape, ovate to elliptic, 0.8–0.9 the length of ventral lobe, 0.7–0.9× area of the ventral; apex broadly acute to rounded, with denticulation and (often) an apiculus like the ventral lobe; dorsal (free) margin broadly arched, contracted to the base, the teeth similar to those of the ventral lobe. Marginal teeth unicellular, formed of sharply projecting marginal cells, or consisting of a narrower conical projection of the exposed wall of the marginal cells. Cells of median portion of ventral lobe rather short to somewhat elongate-rectangular, 10–11 μm wide × (26)37–48 μm long; subapical and marginal cells moderately thick-walled, the lumen rounded to somewhat angular, the cells 8–13 μm wide and long; cells in distal 0.3 of lobes in ± regular arching tiers; median field of cells in basal 0.5 of leaf narrowly elongate, on both sides of keel (but more so on the ventral side), forming a ± distinct vitta, the vitta variable in length, extending distally (in each lobe) to the lobe middle or a little beyond, the vitta cells reddish pigmented, particularly at the base, with longitudinal walls uniformly thick-walled to sinuous, the transverse walls often thinner, 12–18 μm wide × 39–57 μm long (to 4.5:1); surface coarsely papillose, the papillae rounded to short-elliptic, 2–4 per cell in distal half of lobe, at times with a single papilla equaling the cell lumen in diameter; elongate cells of median base finely striate to coarsely striolate-papillose. Oil-bodies (Schuster, 1968a) in median cells of lobe 2–4 per cell (absent in some cells), rather distinctly botryoidal, spherical and 3.8–4.5 μm in diam. to ellipsoidal and 3–4.5 × 4–6.5 μm. Gemmae infrequently produced, brownish, angular-stellate, 1-celled.

Paroecious, often with several pairs of non-ventricose leaves between androecium and gynoecium. ♂ Bracts below the ♀, rigid like the leaves, similar to leaves in shape and form except ventricose toward base; antheridia short-elliptic to distinctly clavate, 2–3 per bract, the stalk variable (often within one androecium): uniseriate or biseriate throughout, or a combination of uniseriate and biseriate, sporadically 4-seriate throughout, the stalk often broadest immediately below the antheridial head, the stalk cells very thick-walled. Subgynoecial bracts larger than vegetative leaves, similar to leaves except the dorsal lobe wider and typically erect, the innermost bract(s) concave, shallowly bilobed, clasping the perianth base. Perianth elliptic to oblong, contracted to mouth, pluriplicate in distal 0.5, the mouth shallowly and irregularly lobulate, the lobule margin with several sharply angular, mostly 1–2-celled spine-like teeth, the submarginal cells papillose like the leaves; mouth area often whitish and with lobule tips variously withered and eroded.

Sporophyte not seen.

Distribution and Ecology: New Zealand: Stewart Island (960 m), South Island (1160–1970 m), North Island (1630 m); Australia: Tasmania (1450–1490 m), New South Wales (1780–2140 m). In New Zealand known from Fiordland, Southland (Eyre Mtns.), Otago, Canterbury, Westland, Sounds–Nelson and Volcanic Plateau (Tongariro Natl. Park) EPs.

An alpine species throughout its range and terricolous or saxicolous, typically occurring in wet areas such as the margins of tarns and rills, over peaty soil of seepage areas (particularly

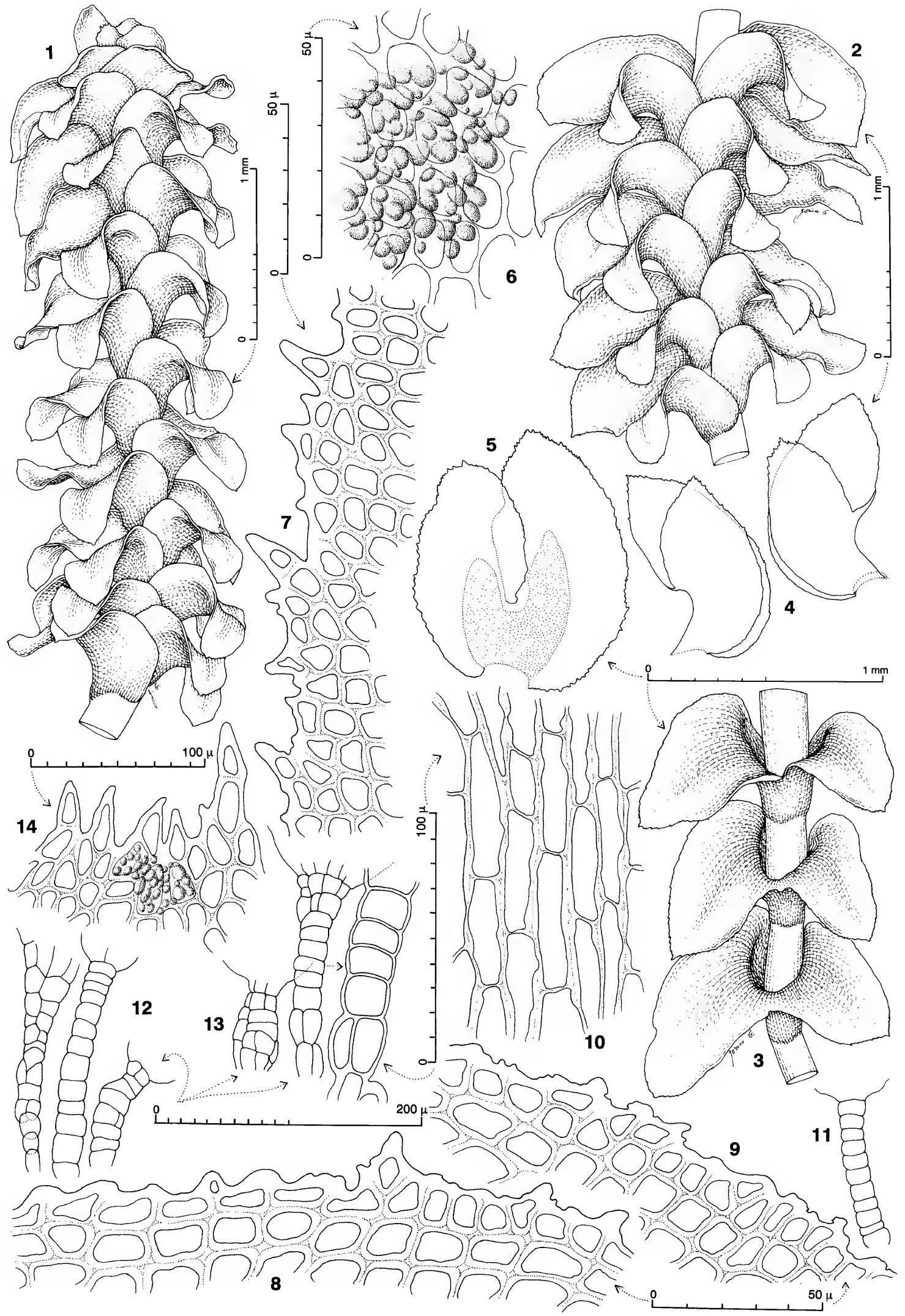

Fig. 164.
Diplophyllum verrucosum R.M.Schust. 1. Sector of shoot, dorsal view. 2. Shoot sector showing four-ranked condition, dorsal view. 3. Sector of shoot, lateral view. 4. Leaves. 5. Leaf with lobes spread, the vitta shown by stipple. 6. Upper-median cells of ventral lobe, with coarse surface papil-

on slopes providing some drainage), on soil over or between stones or boulders. It is found in sedgelands, short tussocklands and cushionfields of *Donatia novae-zelandiae*, *Oreobolus impar*, *O. pectinatus*, *Carpha alpina*, *Chionochloa australis* and *C. crassiuscula*, and is accompanied by *Andreaea acuminata*, *A. nitida*, *Cephalomitrion aterrimum*, *Cryptochila grandiflora*, *Dicranum aucklandicum*, *Drepanocladus aduncus*, *Hygrolembidium acrocladum*, *Isotachis montana*, *Marsupella ustulata* subsp. *childii*, *Nothogymnomitrion erosum*, *Notoligotrichum australe*, *Racomitrium crispulum*, *Radula sainsburiana*, *Rhacocarpus purpurascens*, *Solenostoma totipapillosum*, *Sphagnum cristatum* and *Warnstorfia sarmentosa.*

Comments: When optimally developed, *Diplophyllum verrucosum* is a distinctive plant, with its deep reddish orange color, dorsal and ventral leaf lobes of almost equal size, and both lobes squarrose-reflexed and widely divergent (Fig. 164: 1, 2), forming a distinct "V" when seen in lateral aspect (Fig. 164: 3). It differs from the other New Zealand species in being found in constantly wet and often inundated habitats and in having the densely matted growth habit of *Isotachis montana* or *Cryptochila grandiflora.*

Diplophyllum verrucosum may eventually prove to be conspecific with the southern South American *D. squarrosum* (for a discussion see Engel and Merrill, 1998). It seems advisable to maintain the two species separate until more collections become available, at which time the status of these two species can be reevaluated.

Diplophyllum gemmiparum J.J.Engel & Merrill

[Fig. 165]

Diplophyllum gemmiparum J.J.Engel & Merrill, J. Hattori Bot. Lab. 84: 255. *f. 3*. 1998. Holotype: New Zealand, South Is., Canterbury Prov., Arthur's Pass Natl. Park, area immediately below summit of Avalanche Peak, Scotts Track, W of town of Arthur's Pass, 1650 m, *Engel 22042* (F).

Plants loosely creeping to ascending, clear light green to deep red, but stems dark brownish in older sectors of plant, the ♂ bracts at least faintly reddish tinged, and clusters of gemmae at stem apices reddish orange; basal portion of plants repeatedly branched and soon becoming leafless; shoots small, to 1.8 mm wide. Branching common but irregular, lateral-intercalary, often with numerous subgynoecial innovations. Rhizoids common except near shoot tips, in distinct fascicles (or at least localized) from cortical cells just above the ventral leaf bases, but tending to become somewhat scattered in older portions of shoot. Stems flexuous, with differentiated cortex of 2–3 layers of thick-walled cortical cells; medullary cells thin-walled, colorless; ventral side of stem blackish, infected with dark-pigmented endophytic fungal hyphae. Leaves rigid, dorsally assurgent (particularly when dry), densely imbricate, bilobed, conduplicate-channeled, the basal portion loosely sheathing the stem, the keel 0.55–0.6 the

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lae shown in part. 7. Distal sector of ventral margin of ventral lobe. 8. Base of ventral lobe ventral margin, surface detail not shown. 9. Base of free margin of dorsal lobe, surface detail not shown. 10. Median-basal cells of leaf. 11–13. Antheridial stalks, with detail of portion of a stalk indicated at right in fig. 13 (the antheridia in fig. 12 were obtained from a single inflorescence, the same for fig. 13, fig. 11 drawn to same scale as 12 and 13). 14. Portion of perianth mouth; surface papillae indicated in part. (Figs. 1–11, 14, from type; 12, from *Engel 21982*, New Zealand, South Is., Fiordland EP, head of Gertrude Valley; 13, from *Engel 18557*, New Zealand, South Is., Fiordland EP, plateau and slopes below Mt. Burns.)

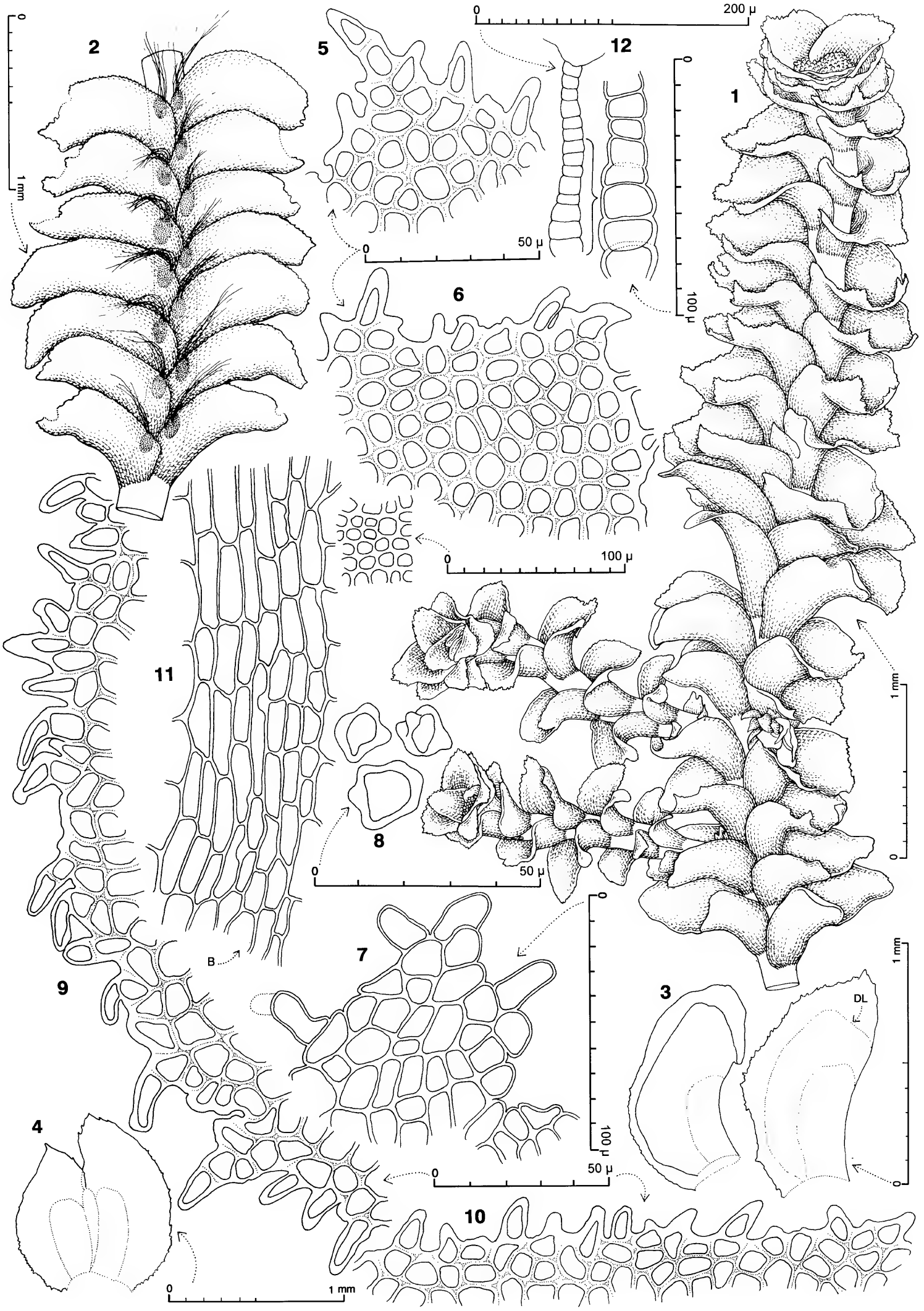

Fig. 165.
Diplophyllum gemmiparum J.J.Engel & Merrill. 1. Main shoot with 2 lateral-intercalary branches, dorsal view; note masses of gemmae at apices of main shoot and lower branch. 2. Sector of shoot, ventral view (note position of rhizoids, the rhizoid pads stippled). 3. Leaves, dorsal and ventral as-

length of leaf, obliquely spreading, rounded in section and not sharp, ± straight to weakly arched, the sinus broadly acute and not reflexed; dorsal and ventral lobes subequal in size but the dorsal always smaller, the ventral lobe plane to weakly reflexed, the dorsal erect to broadly squarrose-reflexed at the tip; lobes truncate and abbreviated in gemmae-producing leaves; leaf insertion ± transverse, the leaf bases overlapping dorsally, extending to more than half the width of the stem, the ventral bases overlapping, particularly in distal portion of shoot. Ventral lobe weakly channeled, typically only moderately reflexed, the margin not decurrent, the ventral half of leaf narrowly to broadly elliptic, at times subfalcate; apex rounded to broadly acute (rarely minutely apiculate), the apices of gemma-producing leaves becoming narrowed, broken and irregular, often with a broad, hyaline, caducous mucro, sometimes with occasional gemmiferous filaments persisting at the apex; ventral margin broadly arched, tapering to the base, the margins distinctly and somewhat irregularly toothed, the teeth somewhat larger near the base; dorsal margin toothed or at times subentire. Dorsal lobe erect to distinctly reflexed, similar to the ventral in shape but somewhat smaller, the insertion transverse, the dorsal half of leaf elliptic, 0.75–0.95 the length of ventral lobe, 0.65–0.9× area of the ventral; apex broadly acute to rounded, similar to that of ventral lobe; dorsal (free) margin broadly arched, contracted to the base, the teeth similar to those of the ventral lobe. Marginal teeth unicellular (at times with a transverse wall near the base), tapering, rounded at the tip, typically oriented ± at right angles to margin, straight to somewhat curved or hooked. Cells of median portion of ventral lobe short-rectangular, 11–14 μm wide × 14–21 μm long; distal portion of lobe densely areolate, the cells small, moderately thick-walled, the lumen distinctly rounded-elliptic to somewhat angular, the apical and submarginal cells smaller, irregularly arranged to aligned in transverse arching tiers, 7.5–9 μm wide × 8–10 μm long; median cells in basal undivided portion of leaf elongate-rectangular, in a broad band on both sides of leaf midline, forming a broad vitta, the cell walls evenly and only moderately thickened (the longitudinal walls rarely feebly sinuous), the vitta typically not extending distally beyond the keel, the cells of vitta 10–13 μm wide × 28–54 μm long (3–5:1); surface very coarsely papillose in distal portion of leaf, the papillae rounded to short-elliptic, 1–3 per cell in submarginal cells of lobes, often with a single papilla equaling or at times exceeding the cell lumen in diameter; elongate cells of median base striolate-papillose. Gemmae aggregated in dorsiventrally flattened buds at the tips of main shoot and branches, the gemmae produced in chains at the tips of uniseriate filaments clustered at the apices of young developing leaves, the production of gemmae often continuing as the leaves mature; gemmae brownish orange, 1-celled, angular to distinctly stellate, 11.5–12.5 μm diam., including papillae.

Paroecious, the ♂ bracts immediately below the ♀. Androecia with 3–4 pairs of ♂ bracts, the bracts ventricose, distinctly pouched, sometimes faintly reddish tinged at extreme base, the margin of dorsal lobe abruptly reflexed at apex; antheridia 2 per bract, the stalk elongate, uniseriate, the basal 2–3 tiers thick-walled. Gynoecia subtended by a pair of leaf-like bracts, the bracts larger than leaves, subequally lobed, erect and sheathing the perianth, sometimes with

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pects, the vitta shown by stipple (DL = dorsal lobe). 4. Leaf with lobes spread, the vitta shown by stipple. 5, 6. Apices of ventral lobe. 7. Apex of dorsal lobe showing mucro. 8. Gemmae. 9. Basal sector of ventral lobe ventral margin. 10. Distal sector of ventral lobe ventral margin. 11. Basal cells of ventral lobe (B = lobe base; keel to left); a few cells from near ventral base of lobe drawn at upper right at same scale. 12. Antheridial stalk, with detail of lower sector shown at right. (All from type.)

a smaller unlobed bract adjacent to the perianth. Perianth elliptic, plicate at least in distal 0.5, at times almost to the base, contracted at the mouth, shallowly lobulate distally, the lobule margins with sharply tapering, 1-celled teeth and denticulations formed by projecting ends of marginal cells; cells in region of mouth subquadrate to short-rectangular, moderately thick-walled, those of perianth proper thick-walled and with a rounded lumen.

Sporophyte not seen.

Distribution and Ecology: Endemic to New Zealand: South Island (1360–1650 m), North Island (2025 m). Known from Canterbury, Westland and Volcanic Plateau EPs, only from three high-alpine sites. The type collection came from deep in a shaded, protected niche between boulders of a rocky outcrop, intermixed with *Diplophyllum dioicum*, *Hepatostolonophora rotata* and *Riccardia* sp. on Avalanche Peak (Arthur's Pass, 1650 m). At Rainbow Skifield (St. Arnaud Ra., Nelson Lakes Natl. Park, 1360–1480 m) in a mosaic of tussock grass and alpine vegetation along with tarns, rills, rocky outcrops and boulderfields, the species forms ± pure, thick patches where thick soil accumulated over an outcrop. In the North Island known only from cliffs and outcrops at 2025 m on the north slope of Mt. Ruapehu, an area characterized by periodic (as recent as 1995) volcanic activity. The ground surface consists of rock, gravel and volcanic cinder. The only vegetation observed in this rigorous habitat were a few bryophytes (confined to cliff and outcrop crevices) and a few scattered high-alpine flowering plants.

Comments: Gemmae of this species are distinctive, stellate-angular, orangish and are produced in terminal buds at the tips of the main shoot and branches (Fig. 165: 1, 8). The gemmae develop in chains on uniseriate filaments issuing from the apices of young developing leaves, although gemmae production often continues on older leaves farther down the shoot; these older leaves will occasionally retain one or more filaments along the margin. Older gemmae-producing leaves typically have the apex contracted to a broad, hyaline mucro, the cells of which are short-rectangular and smooth (Fig. 165: 7). This mucro subsequently breaks off, leaving the leaf with a truncate apex.

Perhaps the most remarkable feature of this species, apart from the abundant production of gemmae (Fig. 165: 1), is the aggregation of rhizoids in discrete bundles adjacent to the ventral bases of the leaves (Fig. 165: 2). This character also occurs in *Blepharidophyllum* and *Clandarium* of the *Blepharidophyllaceae* (see Grolle, 1965f), but terminal, *Frullania*-type branching is lacking, the lobe apices of *Diplophyllum gemmiparum* are not bifid and the leaves have a vitta strikingly similar to that of a number of other *Diplophyllum* species. In older portions of the stem, additional rhizoids often develop from other cortical cells, so that the localized arrangement of the rhizoids is obscured.

Diplophyllum dioicum R.M.Schust.

[Fig. 166]

Diplophyllum dioicum R.M.Schust., Bull. Natl. Sci. Mus. Tokyo 11: 20. 1968. Holotype: New Zealand, South Is., Fiordland Natl. Park, track from Lake Mackenzie to Harris Saddle, Humboldt Mtns., 3800–4000 ft., *Schuster 67-386c* (F).

Plants rigid, brittle, loosely creeping to ascending, dark green to yellowish brown, without reddish pigmentation even in sun forms; shoots strongly dorsiventrally compressed, with the

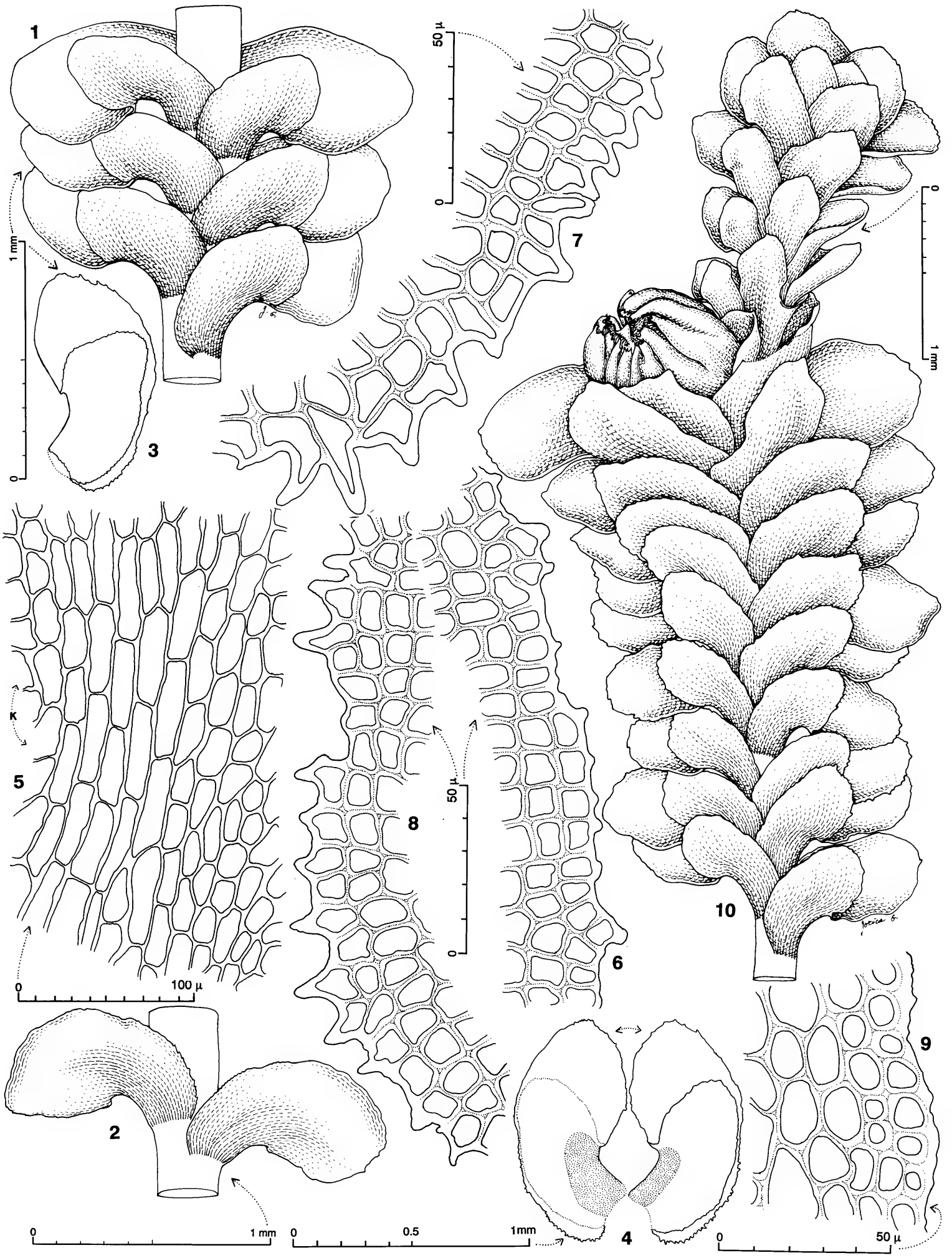

Fig. 166.
Diplophyllum dioicum R.M.Schust. 1. Portion of main shoot, dorsal view. 2. Leaf pair, ventral view. 3. Leaf. 4. Dorsal (right) and ventral aspects of same leaf, the vitta shown by stipple. 5. Basal cells of ventral lobe in sector near keel (= K). 6. Distal sector of ventral lobe ventral margin. 7. Base of ventral lobe ventral margin. 8. Base of free margin of dorsal lobe. 9. Sector of stem, cross section. 10. Shoot with perianth and subfloral innovation. (All from type.)

ventral lobes ± plane, the shoots medium, to 2 mm wide. Branches sparingly developed to frequent, lateral-intercalary. Rhizoids when present scattered on ventral face of stem. Stem stout for plant size, the cortex in 2–4 layers of smaller, thick-walled, yellow-brown cells, the outer layer especially thick-walled. Leaves stiff, contiguous to imbricate, regularly arranged, ladder-like, conduplicate-bilobed, the dorsal lobe ± appressed to the ventral; leaves somewhat dorsally assurgent when dry, when moist horizontal to slightly decurved, widely spreading to squarrose, often distinctly falcate, the keel 0.25–0.35 the leaf length, strongly arched, the sinus abruptly reflexed and sometimes flaring, the opposing dorsal lobes (when leaves imbricate) overlapping, extending to 0.5 the stem width or a little more. Ventral lobe plane or decurved at the tip, the insertion ± transverse, the free margin contracted and subcordate at the base, not decurrent, the lobe elliptic-oblong, lingulate, abruptly contracted at the keel; apex broadly rounded to subtruncate or at times subacute, denticulate, sporadically with a minute, single-celled apiculus; ventral margin broadly and ± symmetrically arched, finely and regularly to somewhat irregularly denticulate (rarely subentire), at times ± repand, the teeth larger near the base; dorsal margin rarely subentire. Dorsal lobe plane, ± appressed to the ventral, asymmetrically ovate to elliptic, 0.65–0.8 the length of ventral, 0.45–0.65 the area of ventral lobe, the insertion ± transverse, not decurrent; apex broadly rounded or at times subacute, sometimes with a minute apiculus similar to that of ventral lobe; dorsal (free) margin ± broadly arched, often contracted at the base, with denticulation similar to that of ventral lobe, but less strongly toothed at the base. Marginal teeth unicellular, consisting of sharp projections of the exposed marginal cell walls, the margins near the lobe bases more sharply toothed (especially the ventral, where sharply spinulose-denticulate). Cells of median portion of ventral lobe ± isodiametric, subquadrate to short-rectangular, 10–14 μm wide × 14–17 μm long; subapical and marginal cells uniformly moderately to distinctly thick-walled, in ± regular arching tiers in distal 0.3 of lobe, 9–13 μm wide and long; basal cells of ventral lobe and keelar region elongate-rectangular, much larger than median cells of lobes, 12–16 μm wide × 35–60 μm long, forming a distinct, sharply delimited vitta equaling the keel in length and ending ± abruptly distally, the longitudinal walls of the vitta cells thickened and sinuous, the transverse walls thin; surface conspicuously and coarsely papillose, the papillae rounded to elliptic, 2–5 per cell; vitta cells finely striolate-papillose. Oil-bodies (Schuster, 1968a) (1)2–5(7) per cell, almost homogeneous in appearance, smooth, colorless, spherical and subspherical, 3–3.5 × 3–4 μm to 5.5–6.5 μm, often ellipsoidal, 4–5 × 5–6.5(7.5) μm. Gemmae almost colorless, 1–2-celled, polygonal, 12 × 14–17 μm to 13 × 13–15 μm.

Dioecious (presumably, but androecia not seen). Gynoecia with 1–3 subfloral innovations; subgynoecial leaves somewhat larger than vegetative leaves but considerably more coarsely armed, those of inner series smaller, deeply concave, shallowly 2–3-lobed. Perianth ovoid to somewhat compressed, strongly and deeply pluriplicate toward the moderately contracted mouth, the mouth decolorate, closely spinulose-denticulate with mostly 1-celled teeth formed of sharply tapered cells, the cells 9–10 × 18–26 μm.

Sporophyte not seen.

Distribution and Ecology: New Zealand: South Island (1000–1830 m); Australia: Tasmania (1200–1490 m). In New Zealand known from Fiordland, Otago, Westland, Canterbury and Western Nelson EPs.

A penalpine–alpine species occurring deep in shaded niches between boulders or over thin soil of damp ledges of rocky outcrops. The species has been found with *Distichium capillaceum*, *Notoligotrichum australe*, *Pohlia wahlenbergii*, *Herzogobryum* spp., *Hygrolembid-*

ium acrocladum, *Lepidozia obtusiloba* and *Andreaea*. Near Kiwi Saddle (Western Nelson EP, 1100 m) it was found on a soil bank under *Nothofagus menziesii* and *Dracophyllum longifolium* forest mixed with *Drucella integristipula*. At Browning Pass (Canterbury, 1400 m) it was in *Chionochloa oreophila – Marsippospermum gracile* tussockland in a seepage, with *Acrobolbus cinerascens*, *Cryptochila grandiflora*, *Dicranoloma robustum*, *Heteroscyphus billardierei*, *Metzgeria furcata* and *Pachyschistochila altissima*.

Comments: *Diplophyllum dioicum* is a very distinctive species due to its strongly dorsiventrally flattened shoots (Fig. 166: 1, 10), regularly spaced, widely spreading, often distinctly falcate leaves, thickish stems (for the plant size) and deep green to yellowish brown color. In contrast to *D. domesticum* and *D. novum*, which have a rather indistinct field of short-rectangular cells extending to the middle of the ventral leaf lobe and sometimes beyond, *D. dioicum* has a distinct vitta, which is largely confined to the keelar region and extends laterally to about the middle of the ventral lobe base, and apically to just beyond the keel (Fig. 166: 4). The vitta also extends laterally into the dorsal lobe but is confined to the vicinity of the keel. The vitta cells are longer than in *D. domesticum* (to 39 μm long in *D. domesticum* vs. up to 60 μm long in *D. dioicum*) and the longitudinal walls are often distinctly sinuous-thickened. In *D. dioicum* the distal half of the leaf is uniformly densely areolate, composed of ± isodiametric cells.

This species is notable for its strongly dorsiventrally compressed shoots, so much so that it is sometimes difficult at first glance to distinguish the dorsal from the ventral side of the plant. The leaves are often distinctly falcate and are very regularly arranged in ladder-like fashion; the plant illustrated by Allison and Child (1975, p. 104) as *D. domesticum* is almost certainly *D. dioicum* judging from the aspect of the shoot, leaf shape and absence of ♂ bracts beneath the gynoecium. This species appears to be dioecious; only relatively young perianths have been seen and androecia are unknown.

Diplophyllum domesticum (Gottsche) Steph.

[Plate 15A; Fig. 167; Fig. 169: 1, oil-bodies, p. 766]

Plants creeping, often closely adnate to substrate, the tips ascending, the plants green to whitish green, deeply reddish orange with exposure; shoots small, to 1.4(1.6) mm wide. Branches occasional to frequent, lateral-intercalary. Rhizoids rather dense, mostly from ventral face of stem, occasionally from near base of ventral lobe. Leaves contiguous to imbricate, conduplicate-bilobed, the dorsal lobe slightly elevated or (var. *icari*) distinctly elevated and squarrose-recurved, the leaves somewhat dorsally assurgent when dry, when moist horizontal, or (var. *icari*) rather strongly dorsally assurgent and then with the shoot appearing concave and channeled in dorsal view, the leaves widely spreading to squarrose, often weakly falcate, the keel 0.25–0.3 the leaf length (0.35–0.5 in var. *icari*), arched, the cells forming the keel with exceptionally thick walls and an often reduced lumen, the sinus abruptly reflexed and the ventral lobe often flaring just distal to the keel, the opposing dorsal lobes (when leaves imbricate) slightly overlapping, extending to 0.5 the stem width or a little more. Ventral lobe plane or the apex broadly decurved, the insertion ± transverse, the free margin not decurrent, the lobe narrowly oblong-elliptic; apex broadly acute to bluntly rounded, denticulate, typically with a distinct, sharp apiculus composed of 1 to several cells and at most terminating in a uniseriate row of 2 cells; ventral margin broadly and ± symmetrically arched, sharply denticulate to irregularly serrulate to the base, the teeth at the immediate base of margin larger, crowded and

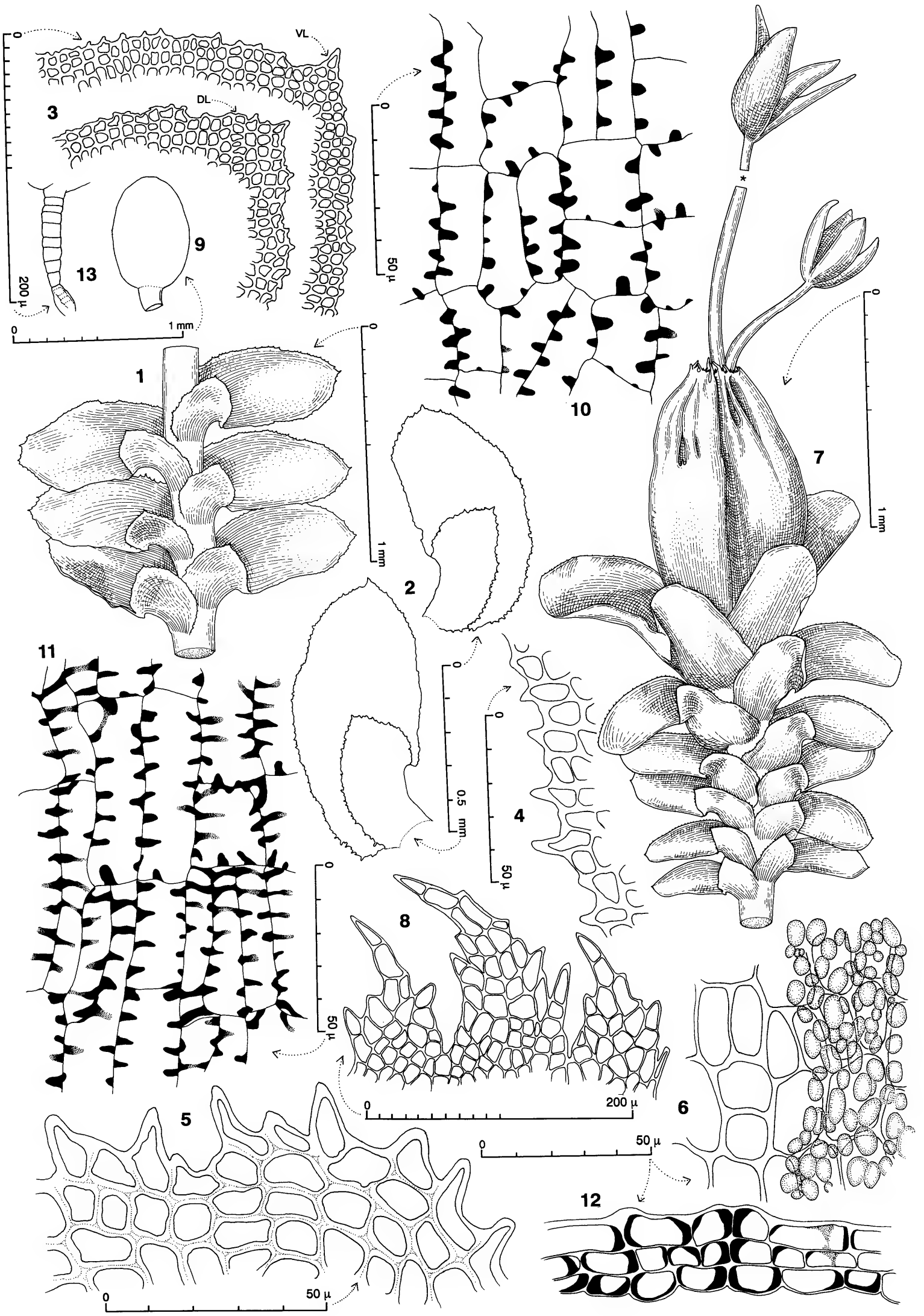

Fig. 167.
Diplophyllum domesticum (Gottsche) Steph. 1. Portion of main shoot, dorsal view. 2. Two leaves. 3. Distal portion of ventral lobe (= VL) and dorsal lobe (= DL). 4. Sector of distal half of ventral

sinuous; dorsal margin often somewhat less strongly armed to subentire. Dorsal lobe plane, asymmetrically ovate to elliptic, 0.5–0.7 the length of ventral lobe (0.75–0.85 in var. *icari*), 0.3–0.45× the area of ventral lobe (0.5–0.7× in var. *icari*), the insertion ± transverse, not decurrent; apex often reflexed, acute (rarely ± rounded), with a distinct apiculus similar to that of ventral lobe; dorsal (free) margin broadly arched, the margins with denticulation similar to the ventral lobe or more pronounced, the free dorsal margin armed to the base, the teeth in basal portion larger and resembling those of ventral lobe base. Marginal teeth variable in size, unicellular, sharply (and often obliquely) projecting, or consisting of narrower conical projections from the exposed wall of the marginal cells, the margins near the lobe bases more sharply toothed. Cells of median portion of ventral lobe short-rectangular, 10–16 μm wide × 19–29 μm long (ca. 2:1 or more); subapical and marginal cells in ± regular arching tiers, ± isodiametric, subquadrate, uniformly thick-walled, 8–10 μm wide × 10–13 μm long, in a more densely areolate broad marginal band, the median field of elongate cells often extending into the distal sector of the lobe, the lobe thus subvittate; median cells in sheathing portion of leaf short-rectangular, 16–18 μm wide × 30–39 μm long, thin or moderately thick-walled, or (var. *icari*) typically narrowly elongate (to 5:1), the longitudinal wall often sinuous-thickened; surface very coarsely papillose, the papillae rounded to elliptic, (1)2–3(4) per cell in distal and marginal cells (sometimes as large as cell lumen); elongate cells of median base finely striolate-papillose. Oil-bodies (see under varieties). Gemmae 1-celled, 11.5–12.5 μm in diam. (including papillae), pale green, polygonal, with thick-walled, tapering protuberances rounded at the summit. Fungal partner a basidiomycete.

Paroecious, the fertile shoots larger. Androecia with (2)3–4 pairs of bracts, the ♂ bracts immediately below the ♀, the dorsal lobes occasionally squarrose, similar to leaves in shape and form except somewhat ventricose toward base; antheridia 1–4 per bract, the stalk uniseriate. Gynoecial bracts somewhat larger than leaves, those of innermost series similar to leaves except the dorsal lobe larger and ca. 0.5 the ventral in size and with the apex rounded and non-apiculate. Perianth typically present, short-elliptic to elliptic-clavate, contracted to mouth, shallowly plurilobulate, the lobule tip rigid, spine-like and terminating in a uniseriate row of 1–2(3) cells, the lobule margins with several sharply angular, mostly 1-celled teeth; gynoecia occasionally with 2 sporophytes.

Capsule ellipsoidal, the wall 3-stratose (exceptionally and then only locally bistratose), 20–26 μm thick, the outer layer of cells equal in thickness to 1.3–1.5 of interior strata; outer layer of cells subquadrate to short-rectangular, without evident two-phase development, the longitudinal walls with nodular to weakly spur-like thickenings, the transverse walls without or with fewer and often smaller thickenings; exposed tangential wall in surface view with an irregular loose reticulum of obscure hyaline wavy ridges that largely obliterates detail of nodular thickenings of outer layer; innermost layer of cells elongate-rectangular, the radial longitudinal walls with nodular to (more often) spur-like thickenings, occasionally tangentially extended into semiannular bands, the bands rather thick for cell size, not forked.

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lobe ventral margin. 5. Base of ventral lobe ventral margin. 6. Median cells of ventral lobe, with coarse surface papillae shown in part. 7. Mature gynoecium showing paroecious condition, dorsal view; note the perianth contains 2 sporophytes. 8. Portion of perianth mouth. 9. Capsule profile. 10. Capsule wall, outer layer. 11. Capsule wall, inner layer. 12. Capsule wall, cross section. 13. Antheridial stalk. (All from *Engel 17575*, New Zealand, South Is., Otago EP, S side of Mt. Cargill, just below summit.)

Spores 9.6–10.1 μm in diam., with low but sharply defined papillose and short-vermiculate markings. Elaters tortuous, 6.2–7.2 μm wide, bispiral.

Distribution and Ecology: New Zealand: Campbell Island, South Island ([75]455–1900 m), North Island (170–1700 m); Australia: Tasmania (960–1490 m), Victoria (1450 m), New South Wales (1780–2140 m). In New Zealand known from Fiordland, Southland (Garvie Mtns.), Otago, Westland, Canterbury (including Banks Peninsula), Marlborough, Sounds–Nelson, Western Nelson, Southern North Island (Akatarawa) and Volcanic Plateau EPs.

The species typically occurs on soil within niches associated with boulders or rocky outcrops and here often is present in crevices or deep in moist, shaded, protected pockets or recesses, as well as over soil under ledges. It is relatively common in the penalpine and alpine zones, and in alpine sites occurs in both fellfields and in tussockland. At the higher elevations it primarily occurs in rock crevice niches but also may be found almost as a pioneer over soil of creek banks and exposed, ice-eroded slopes (1250–1450 m on Mt. Armstrong). The species may occur in forest (but primarily above ca. 750 m) dominated by *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *N. fusca*, *Dacrydium cupressinum* and *Weinmannia racemosa*, accompanied by *Telaranea tuberifera* and *T. tetrapila*. It also occurs on the Volcanic Plateau in the *Leptospermum scoparium – Dracophyllum subulatum* scrub ecotone (near the eastern border of Tongariro Natl. Park, 750 m), or in the South Island mountains on soil banks in penalpine shrublands of *Dracophyllum longifolium*, *D. rosmarinifolium*, *Podocarpus nivalis*, *Ozothamnus leptophyllus*, *Hebe odora*, *H. subalpina*, *Chionochloa flavescens*, *C. pallens* and *Schoenus pauciflorus*. In such penalpine sites it is associated with *Bartramia papillata*, *Ditrichum punctulatum*, *Hygrolembidium acrocladum*, *Notoligotrichum australe*, *Pohlia wahlenbergii*, *Racomitrium crispulum*, *Solenostoma inundatum* and *S. rufiflorum*. In New Zealand the species occurs primarily above 700 m, but may be present at lower elevations in southern sectors of South Island. For example, in South Westland along Cascade Road in the Martyr Saddle area, the species occurs under partial *Blechnum* cover on vertical roadside banks at only 75–110 m, similarly in the Buller River gorge in Western Nelson. The var. *domesticum* tends to occur at lower elevations, but may be found in protected niches in the alpine zone, and the var. *icari* is particularly common in exposed, penalpine–alpine sites.

Comments: *Diplophyllum domesticum* is a common and highly variable species. The lobe apices are typically broadly but sharply acute, with a small but distinct apiculus (Fig. 167: 2, 3), but are at times bluntly rounded and lack an apiculus. Dentition at the apex varies from coarsely and somewhat irregularly serrulate to regularly and finely denticulate. Color ranges from whitish green to an intense reddish orange. Dorsal lobe orientation varies from plane in shade forms to distinctly squarrose-reflexed in exposed situations. *Diplophyllum novum* also has subvittate leaves, with an ill-defined field of rectangular cells extending from the base into the distal part of leaf, but the leaves of *D. novum* are often obliquely inserted in the ventral half vs. ± transversely inserted in *D. domesticum*.

Diplophyllum domesticum almost always bears gametangia (and often sporophytes), so that the paroecious condition is usually evident. Even when antheridia are no longer present, there are at least a few pairs of leaves below the gynoecium with distinctly ventricose bases. Unlike *D. novum*, *D. domesticum* appears to be consistently paroecious; *D. novum* is sometimes observed to produce androecia on lateral-intercalary branches some distance below gynoecia, whereas *D. domesticum* typically forms subfloral innovations that terminate in paroecious inflorescences. *Diplophyllum verrucosum* is also consistently paroecious, but may be readily distinguished by the subequally lobed leaves (Fig. 164: 1–5) with a distinct vitta of narrowly

elongate cells (Fig. 164: 5, 10). *Diplophyllum dioicum* apparently produces gametangia only infrequently, but even when sterile can be distinguished from *D. domesticum* by the more distinct vitta, which is mostly confined to the keelar region, and the absence of reddish pigmentation, even in exposed situations.

The species has two varieties, as follows.

Key to Varieties

1a. Plants light green; leaves ± horizontal, the shoots plane in dorsal view; keel 0.25–0.3 the leaf length; dorsal lobe slightly elevated, 0.3–0.45 the area of the ventral; basal cells in sheathing portion of leaf adjacent to keel short-rectangular (ca. 2.5:1), ± thin-walled; lobe margins and perianth mouth typically green . . . . . var. *domesticum* (p. 761)

1b. Plants deep reddish orange; leaves dorsally assurgent, the shoots concave in dorsal view; keel 0.35–0.5 the leaf length; dorsal lobe often elevated and reflexed distally, 0.5–0.7 the area of the ventral; basal cells in sheathing portion of leaf adjacent to keel typically narrowly elongate (to 5:1), the longitudinal wall often sinuous-thickened; lobe margins and perianth mouth often decolorate and eroded . . . . . var. *icari* (p. 761)

Diplophyllum domesticum (Gottsche) Steph. var. ***domesticum***

[Fig. 169: 1, oil-bodies, p. 766]

Jungermannia domestica Gottsche, Linnaea 28: 548. 1856. *Diplophyllum domesticum* (Gottsche) Steph., Hedwigia 33: 6. 1894. Lectotype (*fide* Engel and Merrill, 1998): Australia (Australian Alps), *F. v. Mueller 144* (BM!).

Plants light green throughout, with shoots plane in dorsal view; leaves ± horizontal, the keel 0.25–0.3 the leaf length; dorsal lobe slightly elevated, 0.3–0.45 the area of the ventral; basal cells in sheathing portion of leaf adjacent to keel short-rectangular (ca. 2.5:1), ± thin-walled. Oil-bodies pale smokey grey, (3)4–7(8) per median cell of ventral lobe, colorless, spherical and 3–5 μm in diam. grading to ellipsoidal and 3–5 × 5.5–6 μm, finely papillose, the globules protruding beyond the membrane; oil-bodies in apical leaf cells 2–3 per cell, at leaf base 5–9(15) per cell; oil-bodies breaking up into fine oil-droplets even before drying.

Diplophyllum domesticum var. ***icari*** J.J.Engel & Merrill

Diplophyllum domesticum var. *icari* J.J.Engel & Merrill, J. Hattori Bot. Lab. 84: 273. 1998. Holotype: New Zealand, South Is., Otago Prov., Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel 17877* (F); isotype: (CHR).

Plants deep reddish orange, the shoots concave in dorsal view; leaves dorsally assurgent, the keel 0.35–0.5 the leaf length, the lobe margins often decolorate and eroded; dorsal lobe often elevated and reflexed distally, 0.5–0.7 the area of the ventral; basal cells in sheathing portion of leaf adjacent to keel typically narrowly elongate (to 5:1), the longitudinal wall often sinuous-thickened; perianth mouth often decolorate and eroded. Oil-bodies occupying a conspicuous portion of cell lumen, hyaline, 6–9 per median ventral lobe cell, coarsely papillose, subglo-

bose to broadly ovoid to broadly elliptic, often somewhat irregularly so, at times with a shallow depression, 5.3–5.8 × 7.2 μm to 3.8–4.8 × 7.2–10.1 μm, spherical ones 4.3–5.3 μm in diam.

Comments: This rather common expression of the species is distinctive, even though it probably intergrades with more typical forms of the species. The dorsal lobes are dorsally assurgent and reflexed and are thus reminiscent of *Diplophyllum verrucosum*. In the latter plant, however, the dorsal lobe is typically subequal to the ventral, and the leaves have a distinct vitta composed of elongate, often deeply pigmented, thick-walled cells. In *D. domesticum* the lobe is subvittate, with a less sharply defined broad median field of short-rectangular cells, often extending into the distal portion of the lobe.

Diplophyllum novum J.J.Engel & Merrill

[Fig. 168]

Diplophyllum novum J.J.Engel & Merrill, J. Hattori Bot. Lab. 84: 274. *f. 8*. 1998. Holotype: New Zealand, South Is., Otago Prov., unnamed peak immediately NE of Mt. Cargill, N of Dunedin, ca. 550 m, *Engel 17589* (F); isotype: (CHR).

Plants rather rigid, prostrate to loosely creeping, rather dull, light green, without reddish pigmentation in sterile portions (perianths sometimes castaneous); shoots medium, to 1.8 mm wide. Branches rather frequent, lateral-intercalary. Rhizoids scattered on ventral face of stem, often dense. Leaves rigid, contiguous to imbricate, conduplicate-bilobed, the dorsal lobe not appressed to the ventral but slightly elevated, the leaves somewhat dorsally assurgent when dry, when moist horizontal to slightly and broadly decurved, spreading at 90° to stem, not falcate, the keel 0.25(0.3) the leaf length, strongly arched, the sinus abruptly reflexed and often flaring, the opposing dorsal lobes (even when ventral lobes imbricate) not overlapping, not extending beyond the stem midline. Ventral lobe plane or the apex decurved, the insertion obliquely succubous, recurved at ventral end, or the ventral margin of lobe cordate to truncate at base and free, not decurrent, the lobe rather narrowly oblong to elliptic, distinctly lingulate, abruptly contracted at the keel; apex broadly rounded to subtruncate or sporadically bluntly acute, finely denticulate to subentire, rarely with a sharp 1(2)-celled apiculus; ventral margin rather straight to weakly arched, finely and regularly to somewhat irregularly denticulate to subentire, often ± repand. Dorsal lobe plane, asymmetrically ovate to short-elliptic, 0.5–0.6 the length of the ventral, 0.25–0.35 the area of the ventral lobe, the insertion ± transverse, not decurrent, the apex broadly rounded to subacute, rarely with a minute single-celled sharp apiculus; dorsal margin weakly arched, the margins with denticulation similar to that of ventral lobe, the teeth of dorsal base not differentiated, the margin ± straight and not contracted at the base. Marginal teeth unicellular, consisting of conical or papilla-like projections of the exposed marginal cell walls, the teeth at the ventral base spinulose, ± straight and sharply tapering, to 3:1. Cells of median portion of ventral lobe short-rectangular, 12–15 μm wide × 19–26 μm long (ca. 2:1 or a little more); subapical and marginal cells ± isodiametric, subquadrate, the walls slightly thickened, with minute trigones, 9–10 μm wide × 11–13 μm long, the median field of short-elongate cells extending into the distal half of the lobe, the lobe thus appearing subvittate, the subapical cells in ± regular arching tiers; marginal row of cells at times with anticlinal divisions, forming an indistinctly differentiated border; median basal cells of ventral lobe larger than the median cells, thin-walled, with minute trigones, 14–16 μm wide × (28)37–40(47) μm long (to ca. 2.5:1); dorsal lobe with a field of short-elongate, large

cells extending laterally from keel to ca. 0.5 lobe width and distally to middle of lobe or a little less than keel length; surface coarsely papillose, the papillae rounded, 2–4(5) per cell in distal and marginal cells; elongate cells of median base finely striate-papillose. Gemmae common, 1-celled, pale green, 11–12 μm in diam., polygonal, with several blunt projections; gemmiparous leaves erose-margined, often with the apex of ventral (and sometimes dorsal) lobe(s) abruptly contracted to a broad, ragged mucro formed of elongate-rectangular cells, the gemmae produced along its margins.

Monoecious, with both paroecious inflorescences and with androecia on lateral-intercalary branches some distance below gynoecia, the androecia subfoliose, the bracts in 2–3 pairs, similar to leaves in shape and form except the dorsal lobe somewhat ventricose toward base and often narrowly reflexed at apex; antheridia 2 per bract, the stalk uniseriate. Subgynoecial leaves gradually increasing in size toward perianth, the dorsal lobe plane or at times ± inflated (these rarely with an antheridium), the bracts of innermost series largest, leaf-like except the dorsal lobe larger and ca. 0.5 the ventral (not smaller, deeply concave, and shallowly 2–3-lobed as in *Diplophyllum dioicum*). Perianth clavate, plicate in distal 0.35(0.5), contracted to mouth, shallowly lobulate distally, the lobules spinose-dentate, the larger teeth with a uniseriate row of 2–3 somewhat elongated cells, intermixed with several 1-celled teeth; cells in region of mouth thin-walled, those of perianth proper distinctly thick-walled and with a rounded lumen.

Capsule short and broadly ellipsoidal, the wall 3(locally 4)-stratose, 28–36 μm thick, the outer layer equal in thickness to the 2 inner layers or a little less; outer layer of cells short-rectangular, with indistinct two-phase development, the longitudinal walls with rather thin, pigmented sheet-like thickenings and well-developed peg- to spur-like thickenings, 4–5 per longitudinal wall, the alternating walls with similar thickenings, but weaker and not or less strongly pigmented, the transverse walls without or with sporadic nodular thickenings; innermost layer of cells elongate-rectangular, the radial walls with nodular to spur-like thickenings, the thickenings often extending onto outer tangential wall as complete, narrow semiannular bands (especially in distal half of valve).

Spores 8.6–9.6 μm in diam., with distinct, sharply defined, broad, sinuous vermiculate markings. Elaters tortuous, 6.7–7.7 μm wide, bispiral to the tips.

Distribution and Ecology: Endemic to New Zealand: South Island (550–800 m). Known from only three sites in Fiordland (Lake McKerrow track), Otago (Mt. Cargill) and Canterbury (Governors Bush) EPs. Occurring in a rock crevice (type) and on a shaded, moist cliff face in a *Nothofagus menziesii* forest (Governors Bush, Mt. Cook Natl. Park, Canterbury). It has been found growing with *Andreaea acuminata*, *Cryptochila grandiflora* and *Ditrichum punctulatum*.

Comments: *Diplophyllum novum* is monoecious, but in addition to paroecious inflorescences, androecia are produced on lateral-intercalary branches some distance below the terminal inflorescence on leading shoots (Fig. 168: 1). This species differs from *D. domesticum* in the broadly rounded to subtruncate lobe apices (Fig. 168: 1, 2, 4, 7); the oblique (ventral half) leaf insertion (Fig. 168: 3); the variable monoecious condition (vs. strictly paroecious in *D. domesticum*); the less strongly armed leaf margins, at times being subentire; and the larger plant size, up to 1.8 mm wide (vs. 1.4 mm wide or less in *D. domesticum*).

The bracts subtending the gynoecia are sometimes inflated at the base, but after a careful examination of numerous shoots these were nearly always empty. In only two instances a single shriveled antheridium was found in the axil of a bract, whereas the antheridia of the androecia on lateral branches of shoots bearing mature sporophytes had not yet dehisced (Fig.

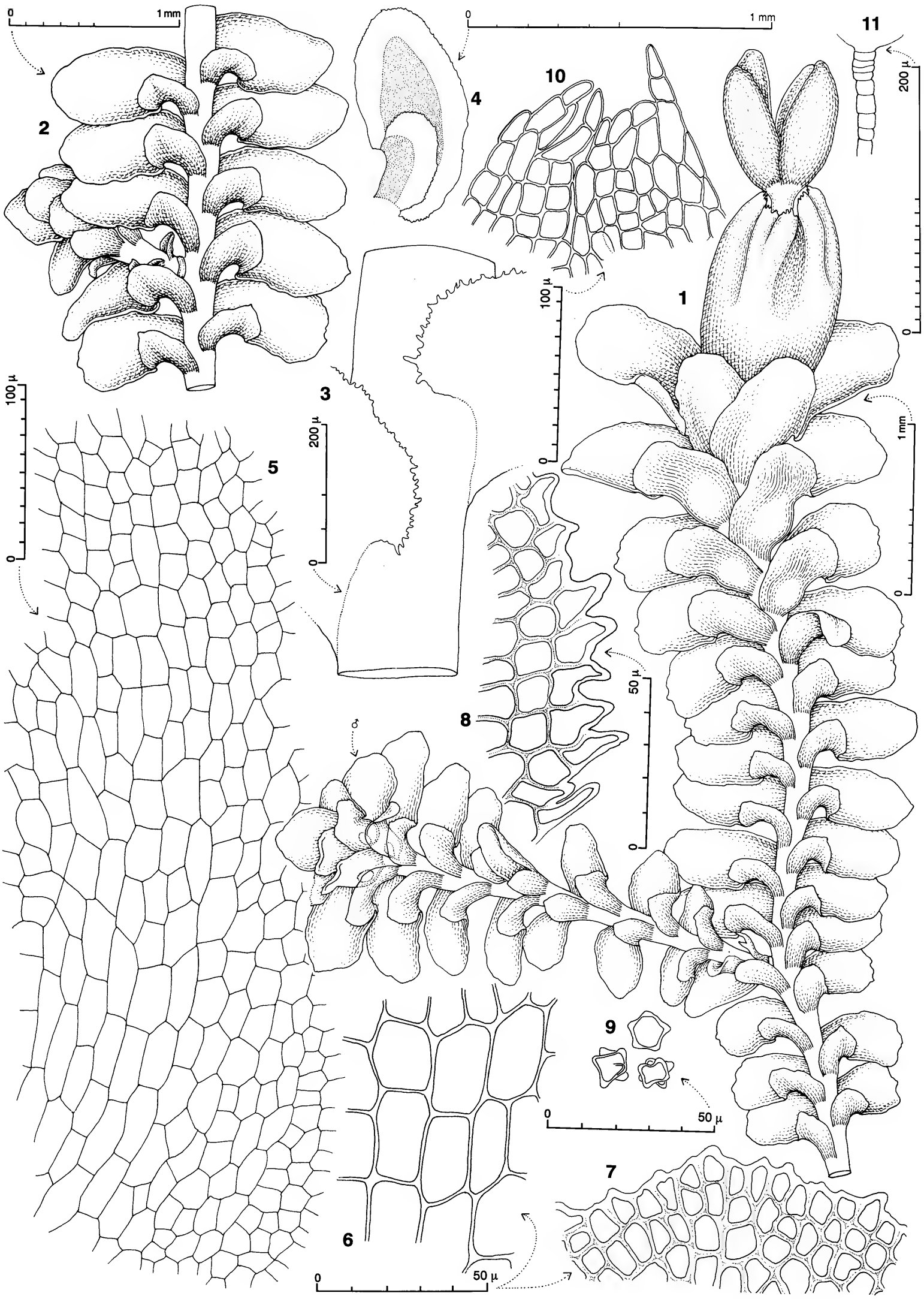

Fig. 168.
Diplophyllum novum J.J.Engel & Merrill. 1. Shoot with a mature sporophyte associated with a paroecious inflorescence, and, below, a leading lateral-intercalary branch with an androecium (♂ = male bract), dorsal view; note mucronate leaf apices indicative of copious gemmae formation.

168: 1, ♂). This suggests that the species may be normally protogynous, with males produced subsequently on lateral-intercalary branches, but can also be protandrous, as in *Diplophyllum domesticum*, with the males preceding the females on the main shoot.

Diplophyllum novum and *D. incrassatum* differ from other Australasian *Diplophyllum* species in the oblique insertion of the ventral half of the leaf (*D. novum*, Fig. 168: 3), the others being ± transverse throughout. The broadly rounded to subtruncate ventral lobe apices and finely denticulate margins of *D. novum* are reminiscent of *D. dioicum*, but the areolation of the leaves is more like that of *D. domesticum*, with a rather broad median field of rectangular cells extending to the middle of the ventral lobe and beyond (Fig. 168: 4, 5). In *D. dioicum* the cells of the distal half of the leaf are uniformly isodiametric, and there is a ± sharply delimited vitta of elongate cells with pitted, sinuous walls, which scarcely exceeds the keel in length.

This species is probably normally green, although perianths in the type are reddish brown pigmented. Assuming that pigmentation is habitat-induced, it is noteworthy that the type is intermixed with plants of *Balantiopsis diplophylla* var. *hockenii* that are distinctly reddish tinged.

Scapania (Dumort.) Dumort.

Scapania (Dumort.) Dumort., Recueil Observ. Jungerm. 14. 1835.

Plants usually loosely prostrate, rarely strongly ascending unless crowded, pale green or reddish brown to purplish, variable in size but mostly vigorous, to 8(10) mm wide, to 25 cm long, the shoots typically strongly dorsiventrally flattened. Branching very sparingly, the branches mostly lateral-intercalary and clearly axillary, but sometimes from ventral end of axil; *Radula*-type, basiscopic terminal branches sporadic; *Frullania*-type branches very rare. Stems with cortex usually well differentiated, in 2–3 layers of small, thick-walled cells, the stems then not or rarely mycorrhizal, the cortex at times hardly differentiated and 1-stratose, then with the medulla often mycorrhizal. Rhizoids usually abundant, scattered, often long and forming a dense mat. Leaves widely spreading in a single plane, the leaf bases not conspicuously sheathing (except in subg. *Buchiella*), deeply complicate-bilobed, ± sharply conduplicate, usually keeled, the keel usually well defined and sharp, weak or rounded in subg. *Scapaniella* and subg. *Buchiella*, diverging from stem from its point of origin, often arched, of varying length (0.1–0.8 the length of ventral lobe), often winged, at least above, the dorsal lobe smaller than the ventral, the leaf insertion in dorsal half at times merely transverse, but in many taxa arched and ± strongly decurrent, ventral half of insertion arched, ± decurrent, often strongly so. Dorsal and ventral lobes usually similar in shape, elliptical-oblong to broadly ovate-rotundate to reniform, with apices rounded to apiculate, the lobe margins usually closely, varyingly, mostly sharply denticulate-dentate (but not serrulate), to sometimes ciliolate or ciliate or entire (in some smaller taxa), the teeth often of strongly differentiated cells. Cells with walls thin (except at times the marginal several rows) to thick-walled, with ±

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2. Portion of sterile shoot with lateral-intercalary branch, dorsal view. 3. Opposing ventral lobe bases showing oblique insertion. 4. Leaf, the vitta indicated by stipple. 5. Portion of ventral lobe showing subvittate condition, the lobe base at bottom, the keel to left, the sector of isodiametric cells at ventral base at lower right. 6. Cells of ventral lobe just below midpoint of lobe. 7. Apex of ventral lobe. 8. Base of ventral lobe ventral margin. 9. Gemmae. 10. Portion of perianth mouth. 11. Antheridial stalk. (All from type.)

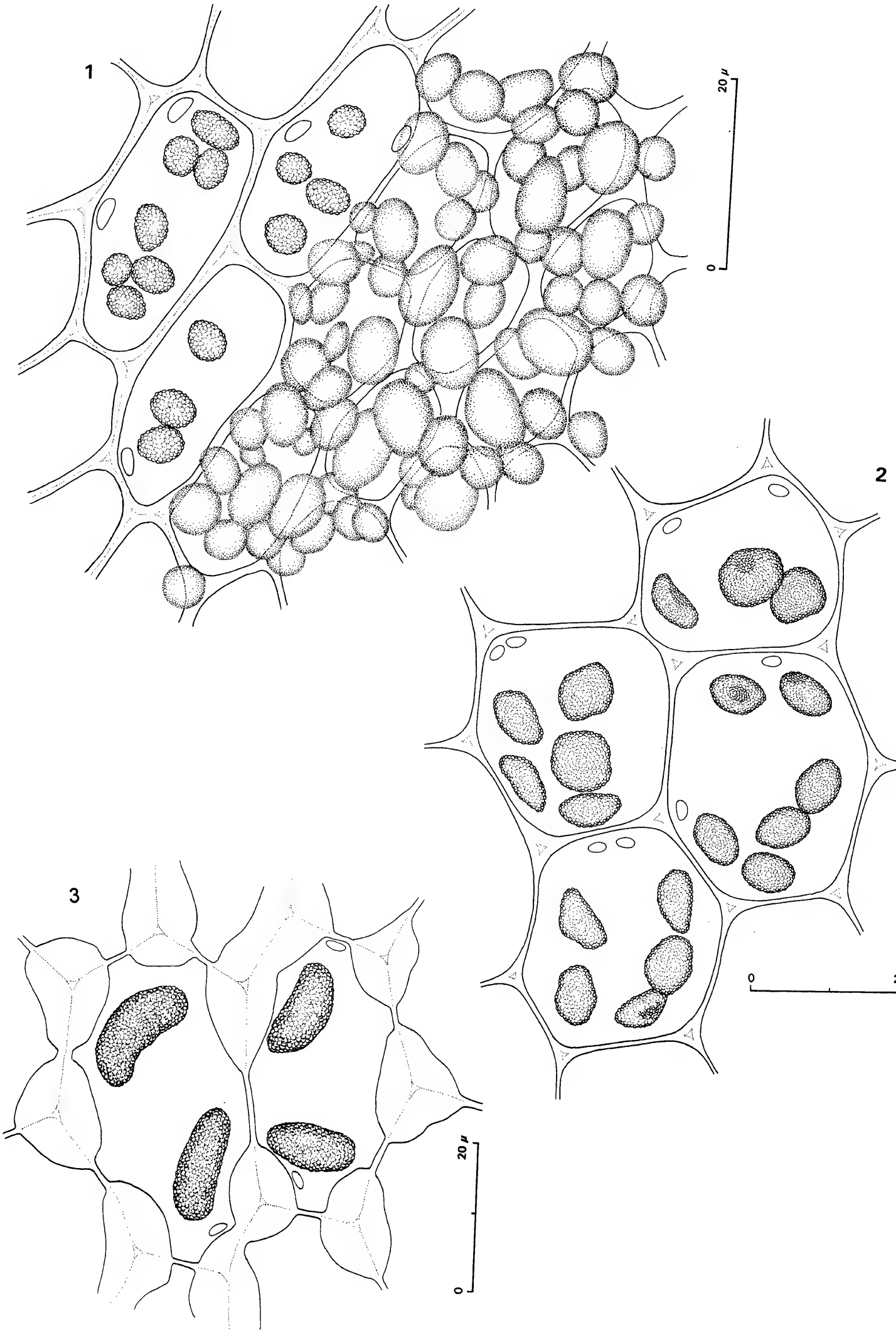

Fig. 169.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Diplophyllum domesticum* var. *domesticum* (Gottsche) Steph. Cells of median sector of ventral lobe, the surface papillae shown on cells at right. 2. *Scapania undulata* (L.) Dumort. Cells of median sector of ventral lobe. 3. *Blepharidophyllum vertebrale* (Taylor *ex* Gottsche, Lindenb. & Nees) Ångstr. Cells of upper-median

well-defined, often nodose trigones; surface smooth or papillose, rarely closely and coarsely so. Oil-bodies (Schuster, 1974a) (1)2–12 per median cell, fine segmented. Asexual reproduction (probably in all taxa) via gemmae, the gemmae 1–2-celled, smooth, ovoid to ellipsoidal, developing from the immature leaf lobes.

Dioecious, rarely (not in ours) paroecious, never autoecious. Androecial bracts leaf-like but somewhat (rarely conspicuously) concave at base, the dorsal and ventral lobes often more nearly equal in size, often without teeth; antheridia (1)2–5, rarely more; paraphyllia often interspersed among antheridia. Gynoecial bracts somewhat larger but not sharply differentiated from leaves. Perianth (few non-Austral exceptions) strongly dorsiventrally flattened, distally parallel-sided, with only (usually sharp) lateral, parallel keels, the mouth wide, truncate, often deflexed, entire or dentate to ciliate.

Seta massive, of numerous undifferentiated cells. Capsule ovoid to oblong-ovoid, the wall (3)4–7-layered; outer layer of cells with strong (sometimes confluent) nodular thickenings; innermost layer of cells with incomplete to complete semiannular bands.

Spores small, usually 1.3–1.6(2)× the elaters in diam. Elaters bispiral.

Type (*cons.*): *Scapania undulata* (L.) Dumort. (≡ *Jungermannia undulata* L.)

A large genus of over 110 species according to Potemkin (1998), 90–100 according to Váňa (1996). The genus has a major concentration of species in the Holarctic. The few tropical species of the genus are restricted to high elevations, e.g., *Scapania portoricensis* Gottsche is endemic to the Neotropics and widespread in mountainous regions. Schuster (1974a) recognized some nine subgenera, and of these, four occur as isolated, often rare elements in Austral areas:

1) subg. *Scapaniella* (Buch) Jörg., with *S. gamundiae* R.M.Schust. of Tierra del Fuego and the maritime Antarctic, where it is exceedingly rare and localized, known from a single collection on Signy Island (Bednarek-Ochyra et al., 2000);
2) subg. *Jensenia* S.W.Arnell, which includes *S. obcordata* (Berggr.) S.W.Arnell, a bipolar species of the high Arctic and exceedingly rare and localized in the maritime Antarctic, known only on the South Orkney Islands and the South Shetland Islands (Ochyra and Váňa, 1989; Bednarek-Ochyra et al., 2000) and also *S. valdonsmithii* R.M.Schust. (*nom. inval.*) of Prince Edward Island;
3) subg. *Scapania*, with *S. nemorosa* (L.) Dumort. and *S. undulata* (L.) Dumort. both of New Zealand. Note also that *S. macgregorii* of New Guinea belongs here.
4) subg. *Macroscapania* R.M.Schust., with *S. cuspiduligera* (Nees) Müll.Frib., reported from Zaire (Váňa et al., 1979) and Lesotho and Natal (Hodgetts et al., 1999). *Scapania hedbergii* S.W.Arnell is endemic to Kenya and *S. esterhuyseniae* S.W.Arnell is known from Uganda and Tanzania. Note that Arnell (1963) does not report the genus (or family) from South Africa.

Potemkin (1998) subdivided the genus into 16 sections, but did not recognize subgenera.

Genus description after Schuster (2002a) but freely modified.

References: Potemkin (1998); Schuster (1974a, 1999c, 2002a).

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sector of ventral lobe. (Fig. 1, from *Glenny 9208*, New Zealand, South Is., Canterbury EP, Temple Basin Skifield track; 2, from *Glenny 9851*, New Zealand, South Is., Otago EP, Rastus Burn; 3, from *Glenny 9108*, New Zealand, South Is., Westland EP, Mt. Brown.)

Key to Species

1a. Dorsal lobes arcuately inserted, distinctly long-decurrent, obliquely reniform-rectangular, the apex (New Zealand plants) obtusely pointed to suddenly apiculate with a sharp tooth . . . . . *S. nemorosa* (p. 771)

1b. Dorsal lobes transversely inserted, not decurrent, orbicular-ovate to oblate-rectangular, the apex (New Zealand plants) mostly subtruncate, occasionally obtuse-rounded . . . . . *S. undulata* (p. 768)

Sect. ***Scapania***

"Gruppe" *Undulata-Dentata* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland 6(2): 432. 1915, *p. p.* Sect. *Undulatae* Buch, Soc. Sci. Fennica, Comm. Biol. 3(1): 135. 1928.

Potemkin (1998, p. 47) pointed out "the correct name of the section is *Scapania*, not *Undulatae*, because its type, *S. undulata*, is the type of the genus."

Scapania undulata (L.) Dumort.

[Plate 15B; Fig. 169: 2, oil-bodies, p. 766; Fig. 170]

Jungermannia undulata L., Spec. Pl., p. 1132. 1753. *Martinellius undulatus* (L.) Gray, Nat. Arr. Brit. Pl. 1: 691. 1821. *Radula undulata* (L.) Dumort., Syll. Jungerm. Europ. 40. 1831. *Scapania undulata* (L.) Dumort., Recueil Observ. Jungerm. 14. 1835. *Plagiochila undulata* (L.) Mont. & Nees in Nees, Naturgesch. Eur. Leberm. 3: 520. 1838. Type: Northern Europe.
For a complete synonymy see Schuster (1974a).

Plants pale to dark reddish brown, rather transparent, 2–4 mm wide, the shoots strongly dorsiventrally flattened. Branching not seen. Stem deep reddish brown (markedly more pigmented than leaves), the cortex well developed, clearly differentiated, 2–3-stratose, of very prominently thick-walled cells; medullary cells larger, thin-walled. Rhizoids not seen. Leaves loosely imbricate, the keel 0.25–0.6 the ventral lobe in length, typically distinctly winged, the wing at times only a narrow strip of tissue, entire, the keel exceptionally with paired wings, the keel slightly, broadly arched inward, the degree of curvature somewhat variable, the keel-stem angle 80–90°. Ventral lobe flat to at most moderately and gently decurved, broadly obovate, 930–2000 μm wide × 1300–2000 μm long, the width (0.70)0.9–1× the length, arching ca. 0.75 across stem to somewhat beyond the stem, the lobe-stem angle 75–85°; apex usually broadly rounded and with teeth ± similar in size and form, the apex with only a suggestion of more prominent tooth and then subapiculate (the more prominent tooth broad-based and with a uniseriate row of 2 cells), the apex sporadically obtusely pointed; margins of lobe entire or subentire in the basal half (of both ventral and dorsal margin), the distal half sparingly denticulate, the teeth at times consisting of 1 tapering or non-tapered cell at most only slightly longer than wide, or the teeth 2 cells long and 1–2 cells wide at base, the terminal cell rounded or angled; ventral margin at base narrowed into a gradually attenuated, long-decurrent strip. Dorsal lobe with insertion transverse, the lobe ± plane to slightly convex for most of its length but the distal sector sharply decurved, 0.55–0.65 the ventral in size, orbicular-ovate to oblate-rectangulate, the width 1.1–1.3 the length, arching across and well beyond stem, the apex

mostly subtruncate, occasionally obtuse-rounded, the apex and distal sector of free margin sparingly crenulate by 1–2-celled teeth or by an angular projection of the exposed wall; free margin not decurrent at base. Cells of median sector of ventral lobe with bulging trigones and thin intervening walls, 16–22 μm wide × 19–31 μm long; marginal cells (median sector of lobe) slightly firm-walled and with bulging trigones, often with bulging septa, a border not differentiated, the cells subisodiametric, 14–18 μm wide and long; surface striate-papillose. Oil-bodies occupying moderate portion of lumen, hyaline and somewhat glistening, 3–6(7) per median cell of ventral lobe, coarsely granular, globose to ovoid to broadly elliptic, a few subdeltoid in profile, often irregular in shape, often with a depression or irregular fold or crease, 3.8–5.8 × 7.7–10.1 μm, a few 6.7 × 10.6–11.5 μm or 3.8–4.8 × 10.6–12.5 μm, subglobose ones 4.8–5.8 μm in diam. Chloroplasts rather large. Gemmae, when present, produced in short chains from immature leaf lobes, 1-celled, broadly ovoid to ellipsoidal.

Androecia and gynoecia not seen.

Distribution and Ecology: Bipolar, in the Holarctic occurring throughout the subarctic well into the Arctic; apparently incompletely circumboreal-circumpolar, since it appears absent from Siberia (cf. Schuster, 1974a for comments on distribution). In the Southern Hemisphere known from two South Island collections, both from Otago EP: Old Man Ra., 1340 m, in alpine flush in a sedge–moss bog (5/10/66, *T. Daly 14609*, dupl. ex herb. G. A. M. Scott [JE!]), and Remarkables, Rastus Burn Skifield, 1630 m, found in a flush through *Chionochloa pallens* tussockland, in an *Oreobolus pectinatus* cushionfield, with *Psychrophila obtusa*, *Celmisia discolor*, *Marchantia foliacea*, *Bartramia papillata* and *Euchiton mackayi* (WELT H10109!).

Comments: We refer the New Zealand population to *Scapania undulata* with some hesitation. On the one hand plants from New Zealand have several characters that define *S. undulata*, such as the ventral lobe narrowed at the base into a gradually attenuated, long-decurrent strip (Fig. 170: 3), and the dorsal lobe insertion transverse with the free margin not decurrent (Fig. 170: 1, 2). On the other hand, the New Zealand and Northern Hemisphere populations differ in a number of respects, as follows.

Key to New Zealand vs. Northern Hemisphere populations

1a. Median cells of lobes with bulging trigones; lobes without a border of thick-walled cells; surface striate-papillose; gemmae 1-celled . . . . . New Zealand population

1b. Median cells of lobes with concave-sided trigones; lobes with a border of prominent thick-walled cells; surface nearly smooth; gemmae 2-celled . . . . . Northern Hemisphere population

The description of the species is based on a small specimen from New Zealand very kindly sent to the senior author by the late Riclef Grolle, and two collections at WELT and CHR.

Sect. ***Nemorosae*** (Müll.Frib.) Buch

"Gruppe" *Nemorosae* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland 6(1): 155. 1905, *p. p.*
Sect. *Nemorosae* Buch, Soc. Sci. Fennica, Comm. Biol. 3(1): 152. 1928. Type: *Scapania nemorosa* (L.) Dumort.

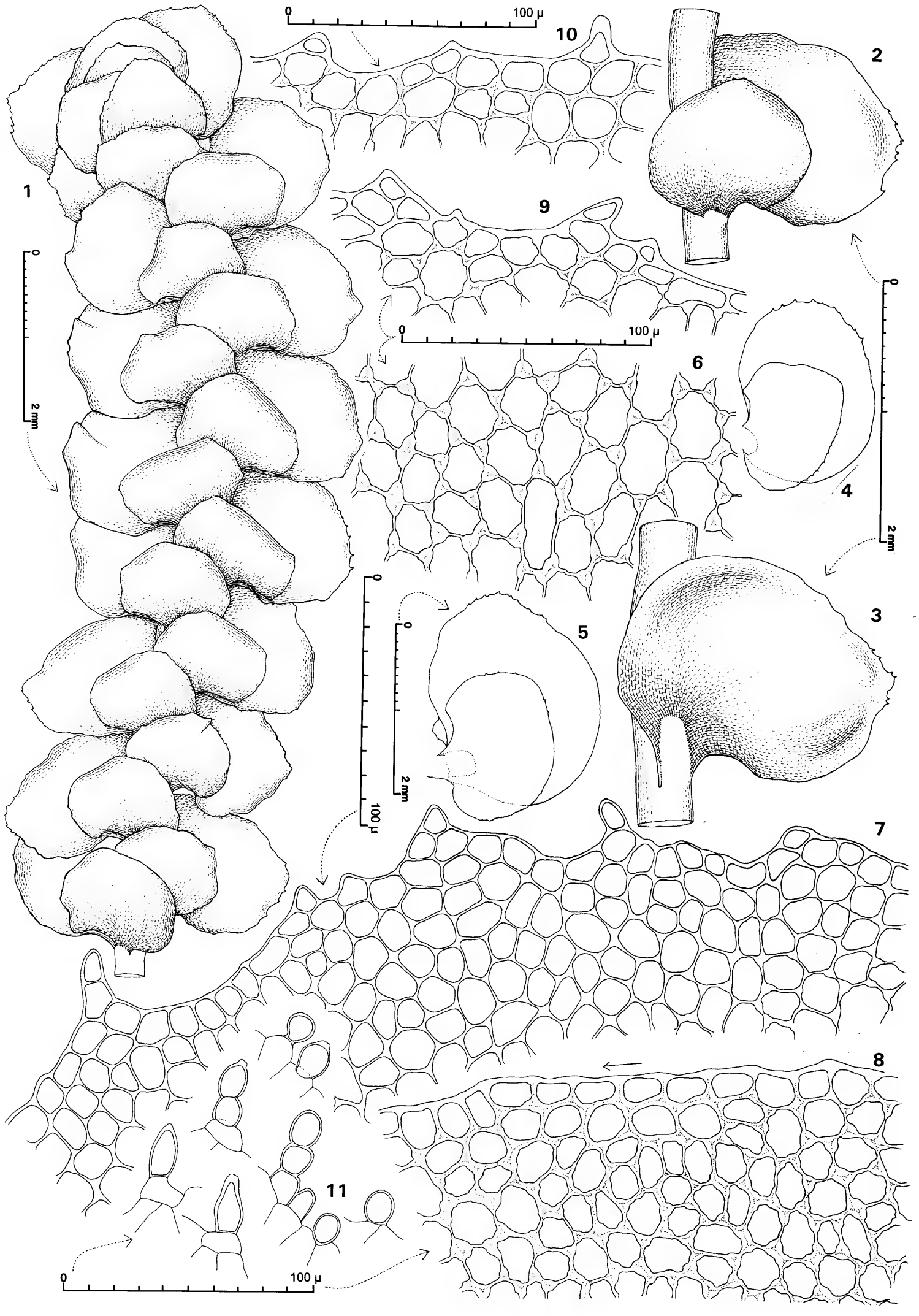

Fig. 170.
Scapania undulata (L.) Dumort. 1. Portion of shoot (dorsal view); note keelar wings. 2. Leaf, *in situ*, dorsal view. 3. Leaf, *in situ*, ventral view. 4, 5. Leaves, note keelar wings (both drawn to same scale). 6. Median cells of ventral lobe (surface papillae not shown). 7. Sector of apex of ventral

Scapania nemorosa (L.) Dumort.

[Fig. 171]

Jungermannia nemorosa L., Spec. Pl. p. 1132. 1753. *Martinellius nemorosus* (L.) M.Bernet & Gray *in* Gray, Nat. Arr. Brit. Pl. 1: 692. 1821. *Radula nemorosa* (L.) Dumort., Commentat. Bot. 112. 1822; Syll. Jungerm. Europ. 41. 1831. *Scapania nemorosa* (L.) Dumort., Recueil Observ. Jungerm. 14. 1835. *Plagiochila nemorosa* (L.) Mont. & Nees *in* Nees, Naturgesch. Eur. Leberm. 3: 524. 1838. *Martinellia nemorosa* (L.) Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 13: 354. 1874. Type: Europe.

For a complete synonymy see Schuster (1974a).

Plants tinged with pale brown, the stem tips at times tinged purplish, to 4 mm wide, the shoots dorsiventrally flattened. Branching sparingly, the branches lateral-intercalary. Stems deep reddish brown, the cortex in 2–3 layers of very thick-walled, pigmented cells; medullary cells thin-walled, with small corner thickenings. Rhizoids abundant, scattered, in a narrow strip on ventral side of stem and forming a dense, narrow, ridge-like mat. Leaves loosely imbricate, the keel (0.15)0.25–0.35 the ventral lobe in length, without a wing or the wing a short, irregular strip of only a few cells wide, the wing not running the length of the keel, the keel weakly but distinctly arched, the keel-stem angle ca. 60–90°. Ventral lobes moderately to rather strongly convex, the ventral margin sometimes rather sharply deflexed, particularly in basal half, the margin in the basal sector oriented stiffly ventrally or even toward the opposing margin, the deflexed sector extending basally to the extremity of the insertion so that the dorsal surface of the ventral lobe is visible in ventral view, the lobes broadly elliptical-subobovate, 1500–2100 μm wide × 2000–2500(2900) μm long, the width 0.65–0.8× the length, not or moderately arching across but not beyond stem, the lobe-stem angle ca. 60–90°; apex broadly and evenly rounded or feebly angled, without or with differentiation of a somewhat more prominent tooth, the more prominent tooth broad-based, with a uniseriate row of to 3 cells and, below, 1–2 pairs of opposing spinose teeth; lobe margins except near bases (of both ventral and dorsal margin) regularly, sharply, rather closely spinose-dentate, the teeth 2–4(5) cells long and 1–2 cells wide at base, the terminal cell rather sharply tapering to the summit, ca. 2.5× longer than wide, the teeth (especially those below) at times consisting of 1 tapering cell; ventral margin rather sharply narrowed toward base, the base narrowed into a gradually attenuated, entire, long-decurrent strip that extends below the level of the keelar insertion. Dorsal lobe with insertion oblique, arcuate, the lobe moderately convex, obliquely reniform-rectangular, the width 0.95–1.4 the length, arching across and considerably beyond stem, rather suddenly narrowed to the oblique base, 0.45–0.55 the ventral in size, widest at or below middle, the apex obtusely pointed to suddenly apiculate with a sharp tooth, the free margin ± toothed in distal ca. 0.5, the basal half entire, the non-free margin armed throughout or the basal half entire, the teeth of dorsal lobe similar to those of ventral lobe, free margin distinctly decurrent at base. Cells of median sector of ventral lobe thin-walled, trigones lacking, 19–25 μm wide × 24–30(36) μm long; marginal cells (median sector of lobe) firm-walled, without trigones, forming a weakly differentiated border 3–4 cells broad, the marginal cells with dilated septa;

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lobe. 8. Sector of ventral margin of ventral lobe. 9. Sector of apex of dorsal lobe. 10. Sector of free margin of dorsal lobe. 11. Gemmae (= double-walled cells) and adjacent cells of young leaf lobe. (All from *T. Daly 14609*, New Zealand, South Is., Otago EP, Old Man Ra.)

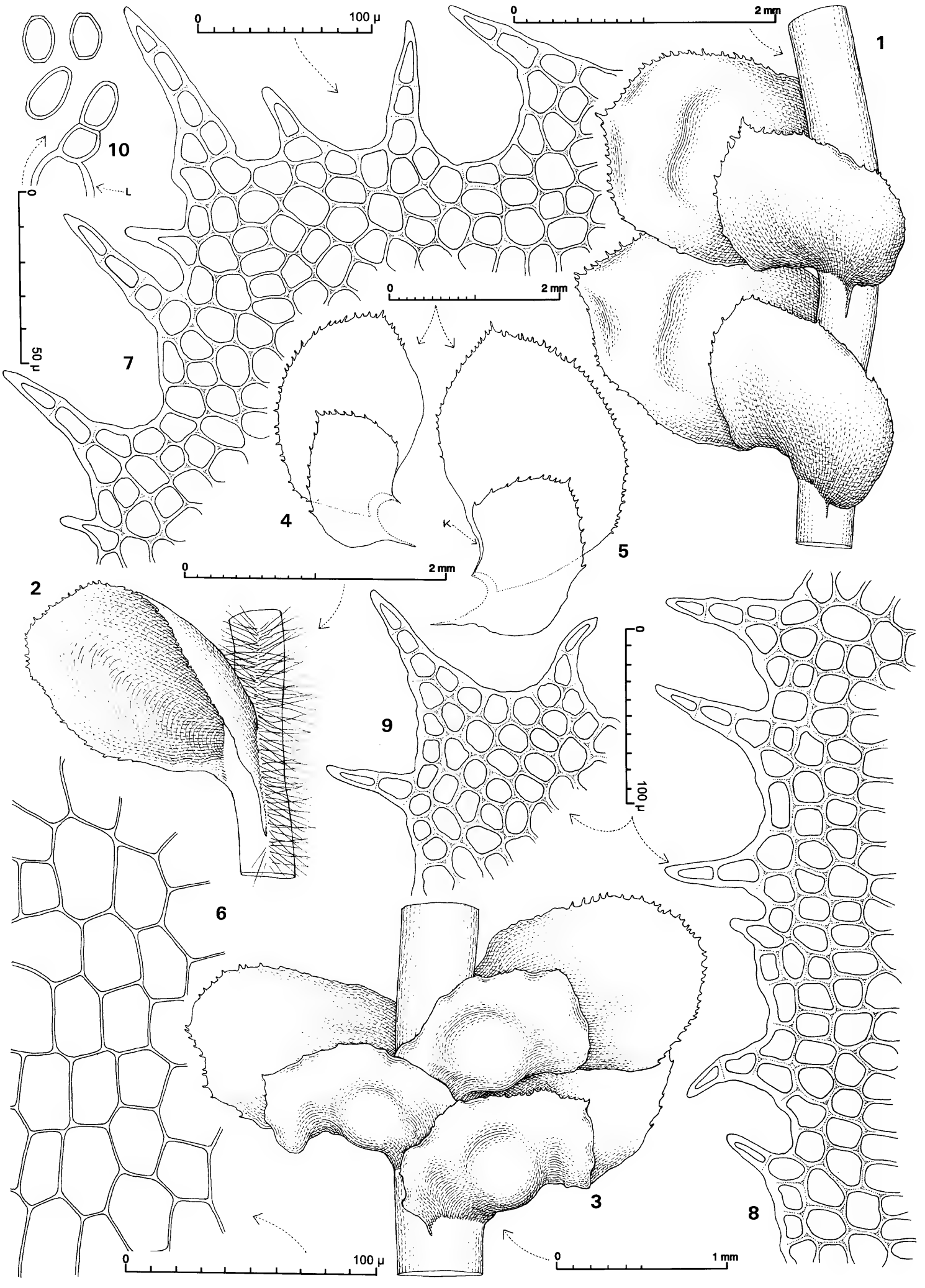

Fig. 171.
Scapania nemorosa (L.) Dumort. 1. Leaves, *in situ*, dorsal view. 2. Leaf, *in situ*, ventral view. 3. Sector of leading shoot with 3 androecial bracts. 4, 5. Leaves (K = keel). 6. Median cells of ventral lobe (surface papillae not shown). 7. Distal sector of ventral lobe. 8. Sector of median-ventral margin of ventral lobe. 9. Distal sector of dorsal lobe. 10. Gemmae (L = leaf cell). (All from *Bartlett 30091/c*, New Zealand, North Is., Southern North Is. EP, NW Ruahine Limestone Plateau.)

surface striate-papillose. Gemmae pale brownish, 1-celled, ellipsoidal, 9.6 × 13.4–17.8 μm. Fungal partner absent.

Dioecious. Androecia terminal but becoming intercalary, the bracts with dorsal lobe ± transversely inserted, inflated, the margins subentire or with several teeth distally, the ventral lobe much larger, dentate distally; antheridia 5–6 per bract; paraphyllia numerous among antheridia, rather long, 1–2-seriate. Gynoecia not seen.

Distribution and Ecology: Bipolar, in the Holarctic occurring from 30–55° N, and common in both warm temperate areas and cold boreal forests (cf. Schuster, 1974a for comments on distribution). In the Southern Hemisphere known only from the North Island, northwest Ruahine Limestone Plateau, 1090 m, in seepage in herbfield associated with *Fissidens* spp., *Bryum* spp. and other cryptogams (13/11/1983, *Bartlett 30091/c* [JE!]).

Comments: The New Zealand population compares rather well with Northern Hemisphere populations of *Scapania nemorosa*. For example, our plants have several characters that define *S. nemorosa*, namely the distinctly arcuately inserted ventral lobe, with the decurrent strip extending below the level of the keelar insertion (Fig. 171: 2); the oblique, arcuately inserted dorsal lobe, with the free margin distinctly decurrent at the base (Fig. 171: 1); the obliquely reniform-rectangular dorsal lobes, with the apex obtusely pointed to suddenly apiculate (Fig. 171: 4, 5); the sharply spinose-dentate leaf margins, with better-developed teeth 2–4(5) cells long and 1–2 cells wide at base, and with the terminal cell ca. 2.5× longer than wide (Fig. 171: 8); the broadly elliptical-subobovate ventral lobes (Fig. 171: 4, 5); and the 1-celled gemmae (Fig. 171: 10).

The New Zealand population is devoid of leaf cell trigones (Fig. 171: 6), while Northern Hemisphere plants have trigones at least concave-sided and they occasionally may be bulging (Schuster, 1974a). Schuster (1974a, fig. 424: 3, p. 578) illustrates cells with minute trigones.

The description of the species is based entirely on a small specimen from New Zealand very kindly sent to the senior author by the late Riclef Grolle.

We follow use of the specific epithet "*nemorosa*" for reasons outlined in Schuster (1974a, p. 577). Grolle (1964a, p. 160) argued for the use of the epithet "*Scapania nemorea*" (L.) Grolle.

Family **BLEPHARIDOPHYLLACEAE** (R.M.Schust.) R.M.Schust. *ex* J.J.Engel

Scapaniaceae subfam. *Blepharidophylloideae* R.M.Schust., Hepat. Anthocerotae N. Amer. 3: 175. 1974. *Blepharidophyllaceae* (R.M.Schust.) R.M.Schust. *in* G.C.S.Clarke & Duckett, Syst. Assoc. Spec. 14: 74. 1980, *nom. inval.*; (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, Fieldiana, Bot. N.S. 25: 108. 1990.

Plants prostrate to erect, light green in shade forms, but with direct light becoming yellowish brown or red-brown to deep brown or (*Clandarium xiphophyllum*) vinaceous. Branching sparing, irregular, predominantly *Frullania* type; *Radula* type present in some species; ventral-intercalary branches also present. Stems with cortex undifferentiated, in 1–2 layers of thin- to rather thick-walled, often brownish cells averaging slightly or distinctly smaller than medullary cells; mycorrhizal infection lacking. Rhizoids usually rarely produced, in fascicles from ventral leaf bases. Leaves fundamentally bisbifid, complicate-bilobed, the keel well defined (*Clandarium*) or the juncture of dorsal and ventral lobes U-shaped in cross section (*Blephar-*

idophyllum), the leaf insertion nearly transverse or on a U- or V-shaped open arc, extending dorsally to stem midline; lobes equal or the dorsal moderately smaller, with apices shallowly bilobed or bidentate (retuse to rounded in *B. densifolium*), the lobe margins variously dentate to ciliate. Cells thin-walled and with nodose trigones (*Blepharidophyllum*) or thick-walled and lacking trigones (*Clandarium*). Oil-bodies dull-opaque, 2 in nearly all cells of lobes, obscurely granular or obscurely finely papillose. Underleaves absent, except when associated with gemma formation (*Clandarium*). Asexual reproduction lacking or (*Clandarium*) via gemmae, the gemmae 2-celled, ovoid, formed in branched, catenated masses from apices of leaf lobes and from lobes of underleaves.

Dioecious. Androecia hardly differentiated; bracts similar to leaves, somewhat ventricose, without a dorsal tooth or lobe; antheridia 2–4 per bract, the body ellipsoid, the stalk 2-seriate. Gynoecia never innovating if fertilized, rarely with a ventral-intercalary innovation if unfertilized; bracts similar to leaves but usually with margins more copiously armed, bilobed like the leaves, with each lobe shallowly bifid. Perianth fusiform, ± dorsiventrally flattened, plicate distally, gradually narrowed toward the mouth, the mouth narrow, ± bilabiate, variously (often strongly) ciliate; perianth polystratose toward base. Sporophyte (known in mature state only for *B. densifolium*). Foot with a conspicuous haustorial, beet-shaped collar, only the collar penetrating tip of shoot. Seta very long, massive, of undifferentiated cells, the outer layer of cells in ca. 30 rows. Capsule long-ovoid to ovoid-cylindrical, the wall 5–6-stratose; outer layer of cells with one-phase ontogeny, the cells with nodular (I-shaped) thickenings on radial walls; innermost layer of cells with semiannular bands.

Spores ca. 16–20 μm in diam., granular. Elaters ca. 8–10 μm wide, bispiral.

Type: *Blepharidophyllum* Ångstr.

A family of two genera, both strictly Austral in distribution. *Blepharidophyllum* has two species, one, *B. densifolium*, is amphi-Atlantic temperate, occurring in South Georgia, the Falkland Islands, southern South America, Kerguelen Island, Crozet, Marion and Prince Edward islands and Gough Island, and the other is found in our area. *Clandarium* has three species, one in our area, while *C. clandestinum* is amphi-Atlantic temperate, found in the Falkland Islands, southern South America and Kerguelen Island, and *C. gottscheanum* occurs in the Falkland Islands and southern South America.

Descriptions of family and the two genera after Schuster (2002a) but heavily modified.

Clandarium (Grolle) R.M.Schust.

Blepharidophyllum subg. *Clandarium* Grolle, J. Hattori Bot. Lab. 28: 65. 1965. *Clandarium* (Grolle) R.M.Schust., Phytologia 56: 68. 1984; New Man. Bryol. 2: 984. 1984.

Plants closely prostrate (except for the erect, microphyllous, gemmiparous shoot apices), usually green or becoming brownish in exposed sites or (*Clandarium xiphophyllum*) rose-red, to purplish even in shade. Branching sparingly, the branches *Frullania* type; ventral-intercalary type occasional (?lacking in *C. gottscheanum*). Stem lacking a clearly defined cortex or (*C. xiphophyllum*) with a 1-layered hyalodermis + 1–2 interior strata of thick-walled cells. Leaves strongly complanate, distinctly complicate-bilobed, the keel well defined, compressed, locally winged, the primary sinus descending 0.6–0.85, the insertion line narrow, transverse or nearly so in dorsal half; lobes unequal, the dorsal slightly to clearly smaller than the ventral, both

lanceolate to ovate or ovate-triangular, shallowly lobulate, the lamina margins copiously ciliate (distally) or spinose-dentate or entire. Cells uniformly thick-walled, without trigones. Oil-bodies dull opaque and hazy in appearance, 2 in nearly all non-ciliiform cells of lobes, obscurely finely papillose. Underleaves lacking in sterile sectors, distinct and to 0.55 the area of leaves in gemmiparous region, in which the leaves are strongly reduced. Asexual reproduction by gemmae, the gemmae in branched chains from lobes of leaves, ovoid to ellipsoidal, 2-celled.

Dioecious. Androecia unknown. Gynoecium terminal on main shoots, those that remain unfertilized nearly always innovated by 1–2(3) ventral-intercalary branches; bracts gradually grading into leaves and scarcely differentiated from them (*Clandarium clandestinum*) or more strongly toothed than leaves; bracteoles lacking. Perianths long-exserted, somewhat dorsiventrally flattened, especially distally, rather strongly narrowed to the mouth, the mouth somewhat contracted, bilabiate, densely dentate to subciliate, the teeth formed of 1–2 moderately elongated, thick-walled cells that taper toward the summit; perianths multistratose in lower sector. Calyptra polystratose in basal 0.1–0.2 and there with archegonia inserted on it, the distal 0.8–0.9 unistratose, a true calyptra present.

Sporophyte known only in immature state in *Clandarium xiphophyllum*. Seta massive, with ca. 22–24 rows of outer cells that are ± larger than the internal cells. Capsule ovoid.

Type: *Clandarium clandestinum* (Mont.) R.M.Schust. (≡ *Plagiochila clandestina* Mont.)

For comments see under family.

References: Grolle (1965d); Schuster (1999c, 2002a).

Clandarium xiphophyllum (Grolle) R.M.Schust.

[Plate 15E; Figs. 172, 173]

Blepharidophyllum xiphophyllum Grolle, J. Hattori Bot. Lab. 28: 65. *f. 3 a–e*. 1965. *Clandarium xiphophyllum* (Grolle) R.M.Schust., Phytologia 56: 68. 1984. Type: Tasmania, Cradle Valley, Pencil Pine River, *Rodway*.

Diplophyllum densifolium fo. *decurvum* Rodway, Tasman. Bryoph. 2: 77. 1916. Type: Tasmania, West Coast.

Plants closely prostrate (except for the erect, microphyllous, gemmiparous shoot apices), yellowish green but often rose-red to vinaceous even in shade, to 3 mm wide, 4 cm long, the shoot tips ventrally decurved. Branching common, the branches long, mostly of *Frullania* type; ventral-intercalary type occasional. Stems with surface striate-papillose, in cross section with a 1-layered hyalodermis of small cells with the exposed wall very thin and (1)2 subhyaloderm cell layers with strongly thickened, sometimes slightly reddish brown walls; medullary cells thin-walled, on average slightly larger. Rhizoids usually present, in bundles from the stem at the ventral base of the leaves. Leaves markedly stiff and brittle, easily tearing, loosely to densely imbricate, bilobed to 0.6–0.75, sharply keeled, the keel ± straight, oriented oblique to stem or nearly at right angles. Lobes at least in the lower part flat and providing a planodiscous leaf arrangement, the lobes ± similar in shape, shallowly lobulate, lanceolate, each strongly arched toward the abruptly narrowed base; apex of each of the main lobes distinctly bifid, the segments caudate, ciliiform, the cilia rigid, terminating in a uniseriate row of 2–3(4), elongate, thick-walled, subcapillary cells with knob-like dilated septa; margins of distal sector of both lobes (especially the dorsal) freely ciliate, the cilia each comprised of one elongated

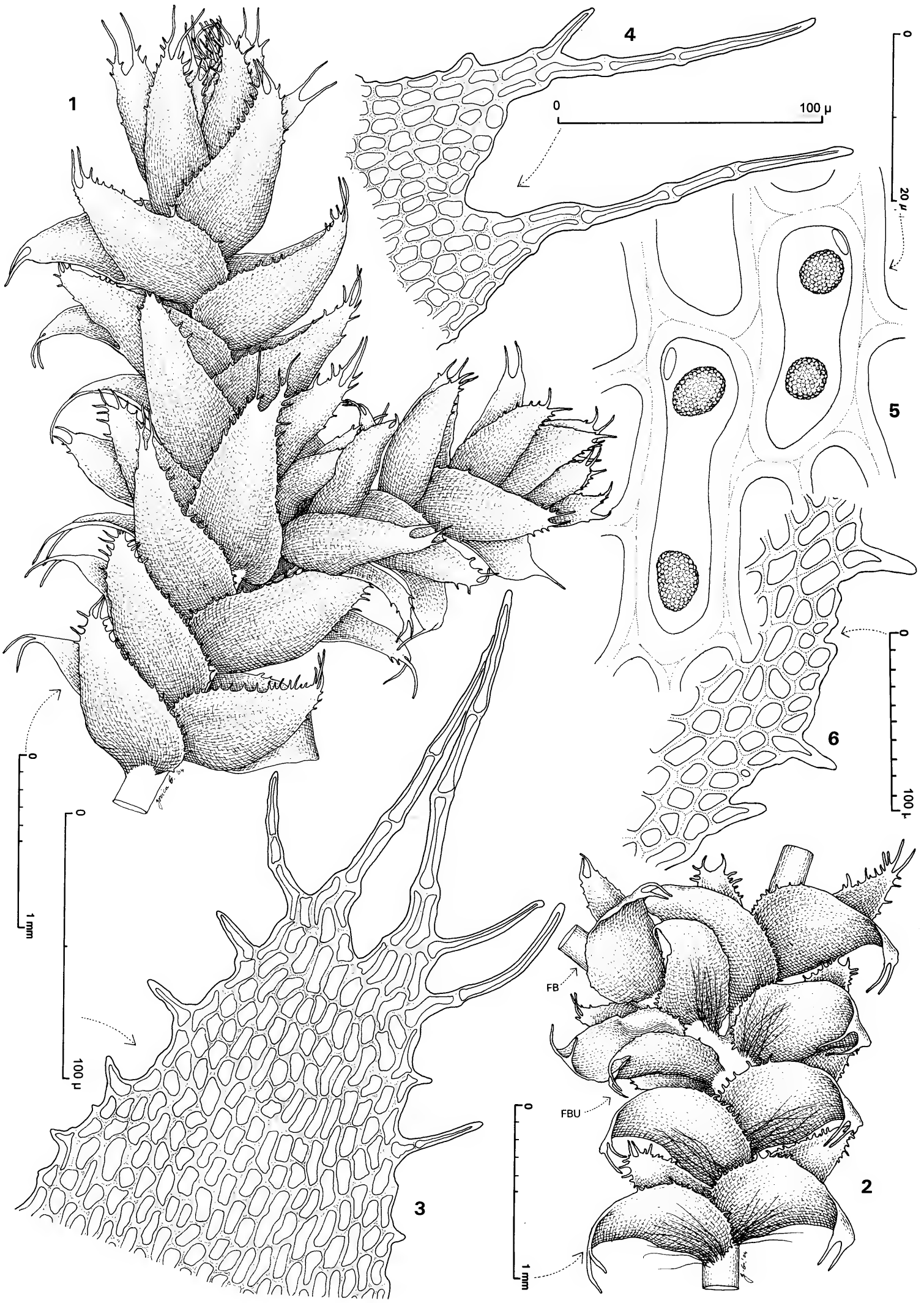

Fig. 172.
Clandarium xiphophyllum (Grolle) R.M.Schust. 1. Portion of main shoot with *Frullania*-type branch (note the short bifid half-leaf), dorsal view. 2. Portion of main shoot with *Frullania*-type branch (= FB), ventral view; note bilobed first branch underleaf (= FBU), unlobed first branch leaf and position of rhizoids on main shoot. 3. Distal portion of ventral lobe. 4. Distal portion of

(mostly 5–8:1) thick-walled cell, the cell markedly thickened at the summit, the margins in median and basal sectors spinose-dentate by unicellular teeth, the margins otherwise crenulate by distinctly dilated septa. Ventral lobe oriented at 70–80° with stem, the distal sector ± basiscopically curved so that the ventral face of the lobe is oriented toward the shoot base. Dorsal lobe ± conspicuously shorter, at an angle of 30–45° with stem, the distal sector plane and hardly curved ventrally or ventrally curved. Cells in median and distal sectors of lobes with strongly thickened walls, the cells at leaf base sometimes with trigones, the median cells of ventral lobe 14–20 μm wide × 23–38 μm long, the basal cells 14–18 μm wide × (36)42–54 μm long; surface conspicuously finely papillose, the papillae at margins (apex to base) isodiametric, the papillae of lobe middle and base somewhat elongated, the papillae at base ± similar to those of lobe middle. Oil-bodies occupying small volume of the cell, dull opaque and hazy in appearance, 2 in nearly all non-ciliiform cells of lobes, even in cells of differing size and shape, 2–4(5) per basal leaf cell, obscurely finely papillose, the globules distinct, the oil-bodies globose to broadly elliptic to linear. Underleaves absent. Asexual reproduction by 2-celled pale gemmae from malformed and reduced leaves and underleaves of gemmiparous apices of main shoot or short *Frullania*-type branches, the gemmae sporadically present; gemmiparous leaves typically small, developing gemmae in catenated branched masses at lobe apices and, at times, from apices of teeth lower on leaf margins; underleaves present at tips of gemmiparous shoots, conspicuous, ovate to ovate-lanceolate, bifid to ca. 0.1–0.4, developing gemmae in a similar manner to leaves.

Androecia unknown. Gynoecia terminal on leading shoots, often with 1–3 subfloral innovations, bracts of innermost series leaf-like except more closely and conspicuously armed, smaller than the next series below, canaliculate, erect (both lobes) and ± tightly appressed to perianth, deeply bifid, the lobes each shallowly bilobed, broader than those of vegetative leaves but grading into them; bracteoles lacking. Perianth distinctly exserted, linear-elliptic in outline, weakly inflated toward base but the remainder clearly dorsiventrally flattened, becoming increasingly so distally, shallowly plicate, the plicae more pronounced in median sector of perianth, the perianth narrowed toward the strongly compressed mouth, the mouth truncate, closely spinose-dentate to subciliate by cells that are free only in distal third grading to entirely free to their bases, the cells elongate (to 6:1), tapering to a sharp, often notably thick-walled summit; cells below mouth markedly thick-walled (particularly the longitudinal walls); perianth 4–5-stratose in basal portion.

For sporophyte see genus description.

Distribution and Ecology: New Zealand: Campbell Island, Auckland Islands (395 m), Stewart Island (365–455 m), South Island (0–1140 m), North Island (835–1280 m), Chatham Islands; Australia: Tasmania. In New Zealand known from Fiordland (Lake Hauroko, Secretary Island, Milford Sound), Westland (Red Hills, Lake Ellery, Haast Pass, Fox River, Gillespies Beach, Hari Hari, Kelly Ra., Hohonu Ra.), Canterbury (upper Wilberforce River), Western Nelson (Sewell Peak), Volcanic Plateau (Mt. Ruapehu) and Auckland (Mt. Moehau) EPs.

A plant of cool humid but not wet conditions. For example, it occurs admixed with *Herzogianthus vaginatus* on steep, moist, peaty, mossy banks in a valley within a low *Nothofagus*

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dorsal lobe. 5. Median cells with oil-bodies. 6. Basal portion of dorsal lobe. (Figs. 1–4, 6, from *Engel 21276*, New Zealand, North Is., Volcanic Plateau EP, Tongariro Natl. Park, Mangawhero R., off Ohakune Mtn. Road, ca. 1200 m; 5, from *Glenny 9107*, New Zealand, South Is., Westland EP, Mt. Brown.)

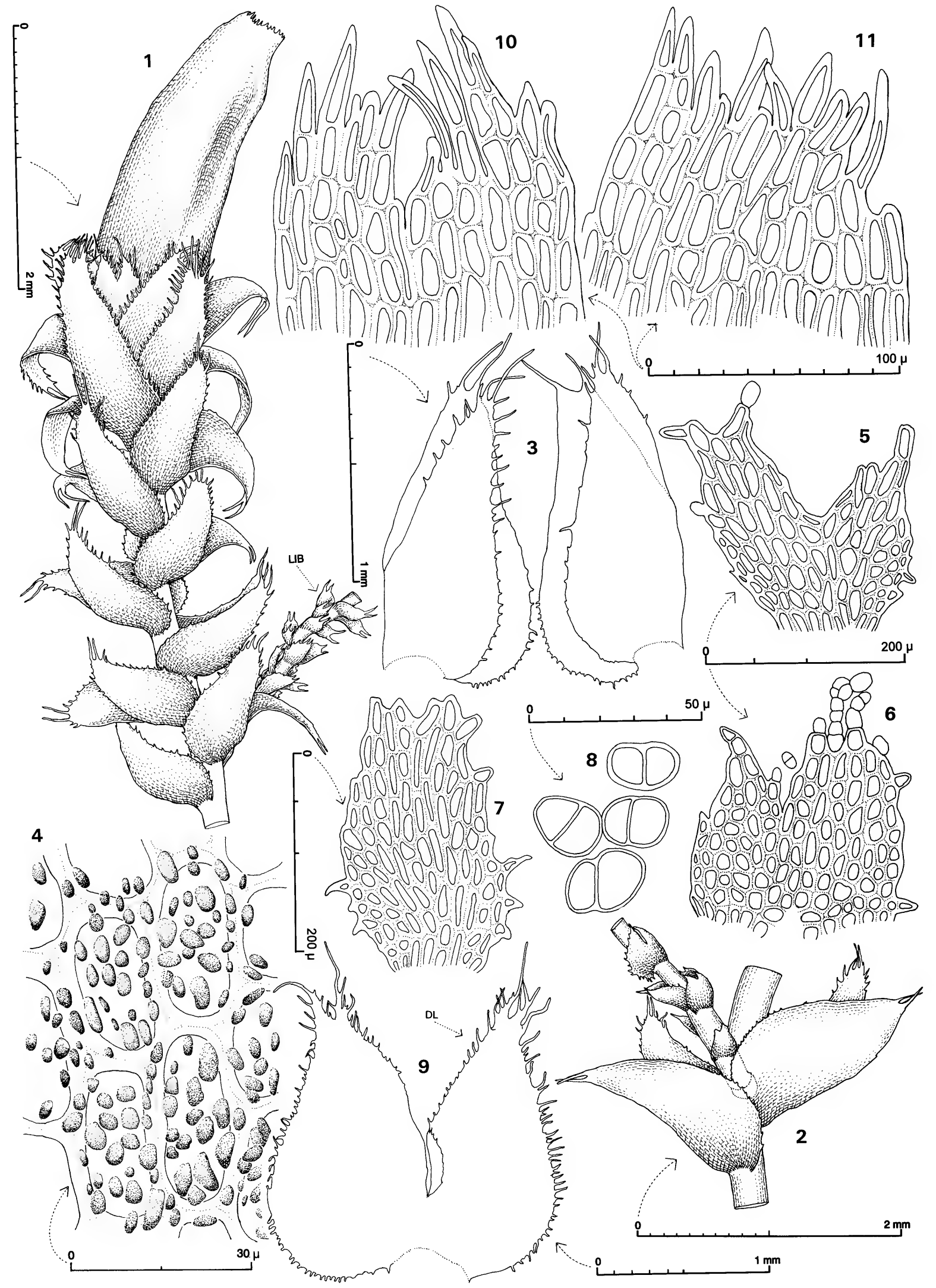

Fig. 173.
Clandarium xiphophyllum (Grolle) R.M.Schust. 1. Portion of leading shoot with perianth and lateral-intercalary branch (= LIB), the branch origin shown in fig. 2; note ensheathing leaf bases. 2. Leading shoot with lateral-intercalary branch originating near ventral end of leaf base, ventral

solandri var. *cliffortioides* forest (bank of Mangawhero River, Tongariro Natl. Park, ca. 1200 m); also on the trunk of *Griselinia littoralis* in a swampy area with *Libocedrus*, *Nothofagus* and *Metrosideros* (ca. 8 km from Ohakune on Ohakune Mtn. Road, Tongariro Natl. Park, ca. 950 m); and as scattered shoots on *Libocedrus* bark in an area with a poorly drained, mucky, fine peat floor in a wet mossy forest of *Lepidothamnus intermedius*, *Ixerba brexioides* and *Dacrydium cupressinum* with occasional *Phyllocladus glaucus* (summit of Table Mtn., Coromandel Forest Park, 835 m). Also on a steep, vertical, shaded, humid but not wet rock in a *Nothofagus menziesii* forest (1 km N of Haast Pass, ca. 520 m). It also was found on rock at the edge of a pool under a rock overhang, in a mosaic of penalpine scrub and alpine vegetation on Arthur's Pass (920 m). In the penalpine zone it can occasionally be found on hillslopes and gullies that are cold and south-facing, under *Chionochloa pallens*, *C. australis*, *Olearia colensoi*, *Dracophyllum longifolium*, *D. rosmarinifolium* tussocklands and shrublands. Occurring on ± open boggy ground (Lake Ellery Track, southern Westland, 30 m) and, according to Schuster (2002a), at sea level at Milford Sound (Fiordland). Associated species are *Acrobolbus lophocoleoides*, *Acromastigum anisostomum*, *A. mooreanum*, *Adelanthus occlusus*, *Bazzania involuta*, *Breutelia pendula*, *Dicranoloma robustum*, *Gackstroemia alpina*, *Kurzia hippuroides*, *Lembidium nutans*, *Lepidozia microphylla*, *L. obtusiloba*, *L. pendulina*, *Leptoscyphus australis*, *Pseudomarsupidium piliferum*, *Radula sainsburiana*, *Riccardia colensoi*, *Schistochila monticola*, *Temnoma quadripartitum*, *Treubia pygmaea* and *Trichotemnoma corrugatum*.

Comments: A distinctive species, with conduplicately bilobed leaves and similar dorsal and ventral lobes united by a rather short keel (Fig. 173: 3). The shoots are rather strongly dorsiventrally flattened (Fig. 172: 1) and in that respect are quite different from *Blepharidophyllum*. Both lobes are shallowly divided at the apex (Fig. 172: 1; Fig. 173: 3), and the distal sector of the main lobes and also the margins of the small lobes have rigid cilia comprised of elongate, subcapillary cells (Fig. 172: 3, 4). Plants frequently developing rose-red to vinaceous pigments, even in shade.

Blepharidophyllum Ångstr.

Blepharidophyllum Ångstr., Öfvers. Kongl. Vetensk.-Akad. Förhandl. 30(5): 151. 1873.

Plants often erect, in exposed sites brownish with age, vigorous, to 3 mm broad, to 10 cm long, the shoot apices distinctly ventrally inclined or cernuous. Branching sparingly or absent, the branches of *Frullania* and *Radula* types; ventral-intercalary branches sporadic. Stems with cortex scarcely to weakly differentiated, the cortical cells considerably or somewhat smaller

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view. 3. Two leaves. 4. Leaf cells (distal third of ventral lobe) showing papillose surface. 5, 6. Leaves from gemmiparous tip, the lower leaf showing gemmae formation. 7. Underleaf from gemmiparous tip (drawn to same scale as figs. 5 and 6). 8. Gemmae. 9. Innermost ♀ bract (DL = dorsal lobe). 10, 11. Portions of perianth mouth. (Figs. 1, 2, 9–11, from *Schuster 53381*, New Zealand, South Is., Westland EP, upper reaches of Haast R., 1 km N of Haast Pass; 3, 4, from *Engel 21276*, New Zealand, North Is., Volcanic Plateau EP, Tongariro Natl. Park, Mangawhero R., off Ohakune Mtn. Road, ca. 1200 m; 5, 7, from *Engel 6610*, New Zealand, South Is., Westland EP, Westland Natl. Park, Gillespies Cook R. Road, between Tornado Creek and Whelan Creek; 6, 8, from *Engel 21331*, New Zealand, North Is., Volcanic Plateau EP, Tongariro Natl. Park, ca. 8 km from Ohakune on Ohakune Mtn. Road, ca. 950 m.)

than the medullary and with walls weakly thickened. Rhizoids often few or none, in fascicles from stem at ventral leaf bases. Leaves complicate-bilobed to ca. 0.6, U-shaped in cross section below juncture of dorsal and ventral lobes, the leaves spatulate, not keeled, the insertion in dorsal half of leaf somewhat, if weakly, incubous, in ventral half of leaf obliquely succubous but the ventral end of insertion arcuate; lobes subequal, ± ventrally secund, narrowly lingulate-lanceolate, with apices narrowed, shallowly bilobed or retuse to rounded, the lobes spinose-dentate to ciliate; lamina margins conspicuously ciliate, at least toward the base. Cells in lobe middle weakly elongated, the walls thin, with nodose trigones; distal cells subisodiametric; surface closely and rather coarsely papillose. Oil-bodies conspicuous, dull opaque, 2 in all leaf cells, granular. Underleaves lacking. Asexual reproduction lacking.

Androecia inconspicuous, hardly differentiated from sterile shoot sectors, terminal but becoming intercalary, sometimes repeatedly so; bracts leaf-like but with the base ventricose, without a lobule; antheridia 2–4 per bract, the stalk 2-seriate. Gynoecia terminal, the unfertilized ♀ rarely innovated by ventral-intercalary branches, a perigynium absent, the bracts free, similar to leaves but larger and with margins more strongly ciliate, divided to 0.5, the lobes each always shallowly bilobed. Perianth long-emergent, narrow-based, fusiform or flask-shaped, slightly dorsiventrally flattened in basal sector, the distal sector more strongly flattened, the upper 0.25 plicate (the plicae not extending to the mouth), the perianth gradually narrowed toward mouth; mouth narrow, truncate, shallowly bilabiate, copiously ciliate, the cilia numerous, flexuous, formed of 1–2 distinctly elongated, narrow, thick-walled cells; perianth 4–5-stratose at base, the distal sector unistratose.

Sporophyte as in family.

Type: *Blepharidophyllum densifolium* (Hook.) Ångstr. *ex* C.Massal. (≡ *Jungermannia densifolia* Hook.)

For comments see under family.

References: Grolle (1965d); Schuster (1999c, 2002a).

Blepharidophyllum vertebrale (Taylor *ex* Gottsche, Lindenb. & Nees) Ångstr.

[Plate 15F; Fig. 174; Fig. 169: 3, oil-bodies, p. 766]

Scapania vertebralis Taylor *ex* Gottsche, Lindenb. & Nees, Syn. Hepat. 72. 1844. *Martinellia vertebralis* (Taylor *ex* Gottsche, Lindenb. & Nees) Trevis., Mem. Reale Ist. Lombardo Sci. Lett. III, 4: 411. 1877. *Diplophyllum vertebrale* (Taylor *ex* Gottsche, Lindenb. & Nees) Steph., Sp. Hepat. 4: 117. 1910. *Blepharidophyllum vertebrale* (Taylor *ex* Gottsche, Lindenb. & Nees) Ångstr. *in* C.Massal., Nuovo Giorn. Bot. Ital. 17: 208. 1885. Type: Tasmania (Insula van Diemen), mis. Dr. Greville.

Plants with a spongy texture, erect, pale green to yellowish to light brown, dull, at times somewhat red-brown, to 3 mm wide, 5 cm long, the shoot apices ventrally decurved. Branching rather frequent, the branches of the *Frullania* type. Stems in surface view finely striate-papillose, in cross section with cortex weakly to moderately differentiated, the cells in 1–2 layers with slightly to moderately thickened, brownish walls, the cells much smaller than those of the medulla; medullary cells thin-walled, but the outer medullary cells with walls feebly thickened. Rhizoids not seen. Leaves usually densely imbricate, obliquely spreading, with

decurved tips, the ventral one slightly basiscopically arched, the orientation transverse, the insertion in the dorsal half slightly less oblique, incubous, in the ventral half oblique, succubous, at the ventral end basiscopically ± curved; leaves with base ensheathing, deeply canaliculate, somewhat bulging-inflated, then suddenly narrowed, when spread broadly ovate, divided to ca. 0.5, the sinus very narrow, acute, the lobes subequal or the dorsal lobe slightly shorter, the lobes broad to relatively narrow, ligulate, the summit of each lobe conspicuously divided into 2 small, acute lobes, the intervening sinus acute to obtuse, rounded at the base, the sinus base often reflexed, margins of leaves from base to apex and also the sinus with numerous pale, often curved, very long cilia, the cilia comprised of a uniseriate row of 2–4 very narrow, long, thick-walled, subcapillary cells, the cilia in basal half of margins ± tortuous, with a uniseriate row of 3–5 cells. Cells with knot-like trigones, the median cells of ventral lobe 24–32 μm wide × 35–37 μm long, median basal cells elongated, 25–30 μm wide × 48–66 μm long; surface densely, relatively coarsely, papillose, even at the leaf base (i.e., the papillae not becoming striate). Oil-bodies conspicuous, dull opaque, in all leaf cells including small, non-elongated basal cell of cilium, otherwise absent in cilia, 2 in all leaf cells except sporadically 3 in cells at leaf base, granular, subspherical to more often elliptic to sublinear to subcrescentic, 5 × 6.5 μm to 5.5–7 × 16 μm, spherical ones 7 μm in diam. Underleaves absent. Gemmae lacking. Fungal partner absent.

Dioecious. Androecia terminal, inconspicuous, very similar to sterile sectors of shoot; bracts ventricose at the base but otherwise very similar to the vegetative leaves; antheridia 2–3 per bract, the stalk 2-seriate. Gynoecia terminal on main shoots, those that have remained sterile sometimes innovating by ventral-intercalary branches; bracts very similar to vegetative leaves, slightly larger, with 2 deeply divided lobes. Perianth conspicuous, long-exserted, ca. 4× longer than wide, the base cylindrical, from the middle weakly dorsiventrally compressed, ± plicate distally, the mouth sometimes decurved, 2-lipped, the lips lobulate, the lobules with numerous long, thick-walled, uniseriate cilia. Calyptra pear-shaped, with sterile archegonia at the base.

Sporophyte unknown.

Distribution and Ecology: New Zealand: Auckland Islands, Campbell Island, Stewart Island, South Island (760–1310 m); Australia: Tasmania. In New Zealand known from Fiordland (Wilmot Pass, Mt. Burns, Manapouri), Westland (Olivine Ra. to Victoria Ra.), Canterbury (upper Wilberforce River, upper Otira valley) and Western Nelson (Matiri Plateau, Garibaldi Ridge, Arthur Ra.) EPs.

It occurs in upper montane forest of *Nothofagus menziesii* and *N. solandri* near treeline, in *Chionochloa pallens* tussockland on cold south-facing slopes and in gullies under *Olearia colensoi*, *Dracophyllum longifolium* and *Podocarpus totara* scrub. In Western Nelson it is found on the sides of marble or limestone sinkholes in the alpine zone. It has been found in *Gleichenia microphylla*, *Carpha alpina* and *Empodisma minus* bog with *Sphagnum australe*, and under *Halocarpus bidwillii* shrubs with *Lepidothamnus laxifolius* and *Carpha alpina*. Its habitat is similar to that of *Clandarium xiphophyllum*, and the two sometimes occur together. Other associated species are *Anastrophyllum schismoides*, *Archeophylla schusteri*, *Bazzania involuta*, *Dicranoloma robustum*, *Eotrichocolea polyacantha*, *Gackstroemia alpina*, *Heteroscyphus billardierei*, *Jamesoniella kirkii*, *Lepicolea scolopendra* and *Riccardia perspicua*.

Schuster (2002a, p. 503) states that the species "is not a lowland plant but occurs chiefly at elevations of 600 m and higher, where it is on soil between and/or over rocks, or sometimes

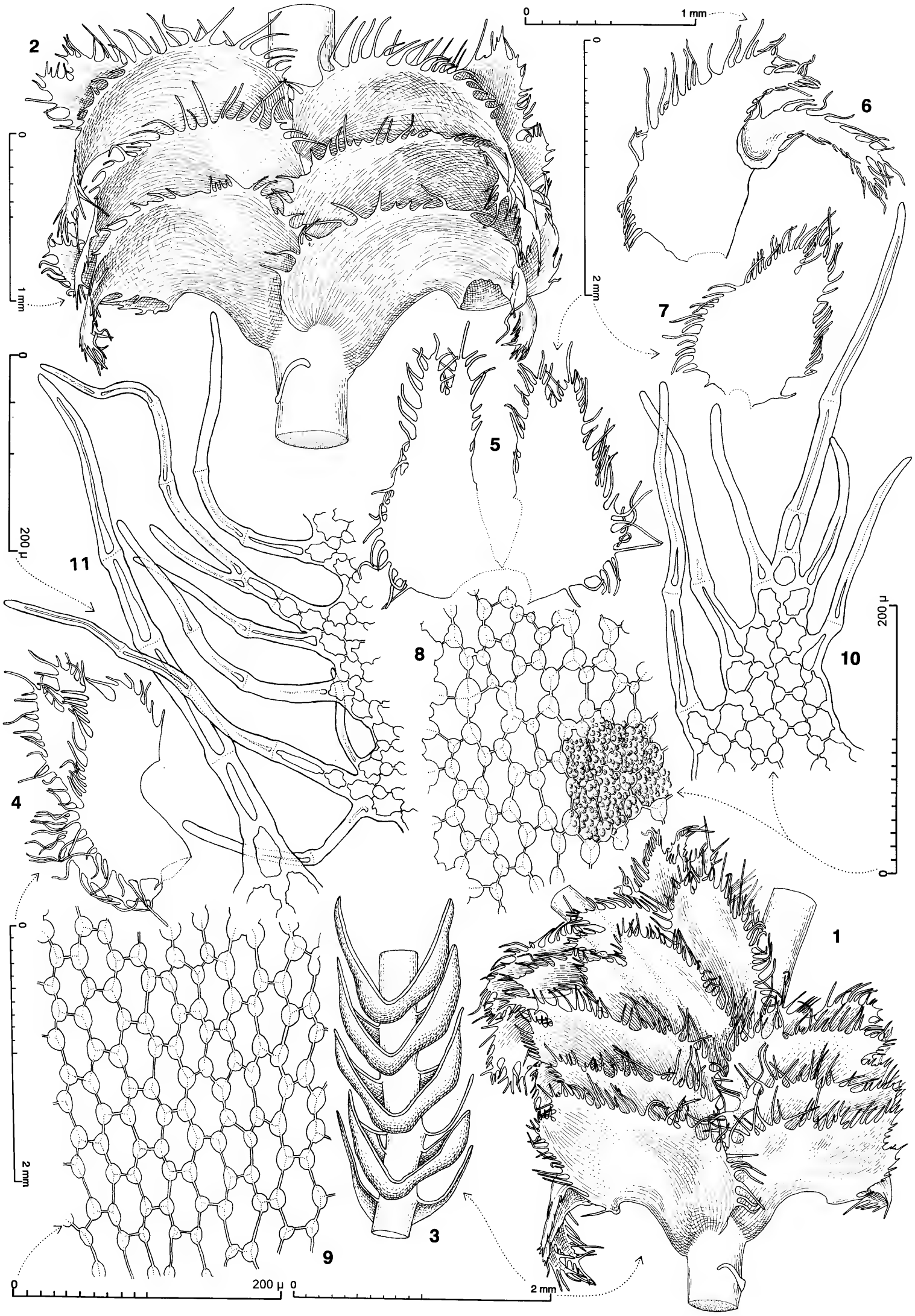

Fig. 174.
Blepharidophyllum vertebrale (Taylor *ex* Gottsche, Lindenb. & Nees) Ångstr. 1. Sector of leading shoot with *Frullania*-type branch and associated half-leaf, dorsal view. 2. Sector of leading shoot,

epiphytic on tree bases" and (p. 504) remarks "it seems largely restricted to alpine slopes where it may occur on decayed culms at the bases of snow tussocks...."

Comments: A distinctive, elegant species that is not likely to be confused with any other of our species. The shoots have a sponge-like texture with leaves densely imbricate (Fig. 174: 1, 2). The leaf base is inflated and U-shaped in cross section (Fig. 174: 3), bisbifid, with each of the two main lobes conspicuously divided at the summit (Fig. 174: 5, 6). The leaf margins, from base to apex, are conspicuously armed with glistening cilia (Fig. 174: 1, 2, 4–6). The cilia each have a uniseriate row of 2–4 narrowly elongated, thick-walled, subcapillary cells (Fig. 174: 11).

Family **GYMNOMITRIACEAE** H.Klinggr.

Gymnomitriaceae H.Klinggr., Höh. Crypt. Preuss. 16. 1858. ("Gymnomitria")
Marsupellaceae Buch, Suom. Maksasammalet 20, Helsinki. 1936, *nom. inval.* Müll.Frib. *in* Rabenhorst, Krypt.-Fl. Deutschland 36: 555. 1954 + 6: 757. 1956, *nom. inval.*

Plants firm, opaque, generally stiffly ascending to erect, sometimes from a creeping caudex, the shoot apices lacking autonomous curvature (except *Prasanthus*), silvery grey or greenish grey, usually developing, at least locally, brown, red, reddish brown or vinaceous pigments, the plants ± determinate in height (except *Herzogobryum* and *Acrolophozia*, which are ± procumbent), small to medium in size, to 3.5 mm wide. Branching of leafy shoots usually from older sectors, the distal sector usually unbranched, the branches lateral-intercalary (from lateral or, more often, ventral half of leaf axils); ventral-intercalary and/or *Frullania*-type branches rare (*Herzogobryum*); *Radula*-type basiscopic branches very rare. Stems firm, the cortex usually in 1(2) layers of slightly to conspicuously thick-walled cells surrounding 2–4 layers of often densely chlorophyllose, often pigmented, thick-walled intracortical cells slightly to conspicuously smaller in size, the intracortical cells typically becoming gradually larger and thin-walled toward the axis middle; stem not dorsiventrally differentiated, without mycorrhizal infection of medulla. Rhizoids scattered, often lacking in upper sectors of leafy shoots, issuing only from stem. Leaves alternate, vertical, varying from stiffly and pectinately spreading to closely and tightly erect-appressed, remote to densely imbricate, ± transversely oriented, the insertion virtually transverse (under 15° succubous), the dorsal end of insertion transverse, extended across and beyond stem midline (lateral merophytes dorsally interlocking), usually bilobed to 0.1–0.4(0.6), rarely emarginate or undivided, almost never trifid; apex and often margins often becoming decolorate and bleached lending a greyish color to the plant, the margins entire or crenulate. Cells firm, the walls thin or somewhat thickened, but usually not evenly thick-walled, the trigones small to large and bulging, the median cells small (usually

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ventral view. 3. Sector of shoot, lateral view; leaves cut off except at their bases to show rounded, keelar portion. 4. Leaf. 5. Leaf with lobes spread (dorsal lobe at left). 6. Leaf. 7. Half-leaf. 8. Median cells of ventral lobe, surface detail shown in part. 9. Median-basal leaf cells (i.e., the median-basal sector of ensheathing or keelar portion; note the non-vittate condition). 10. Distal sector of dorsal lobe. 11. Cilia of dorsal margin of dorsal lobe. (All from *Engel 18404*, New Zealand, South Is., Westland EP, Arthur's Pass Natl. Park, Kelly Ra.)

12–24 μm wide); surface smooth or delicately papillose or (*Acrolophozia*) coarsely papillose. Oil-bodies usually 2–4, rarely 5–6(7) per cell, obscurely to clearly granular, lacking in thick-walled or decolorate marginal cells. Underleaves usually reduced to slime papillae, rarely minute, 2–3 cells wide and acute to subulate, the ventral merophytes usually not more than 2 cells broad. Asexual reproduction absent.

Dioecious or paroecious, less frequently autoecious. Androecia on leading shoots, terminal but usually becoming intercalary, not strongly differentiated from vegetative sectors; bracts usually leaf-like, somewhat more concave, lacking a dorsal-basal tooth, in paroecious species notably larger and with the dorsal margin ampliate and frequently incurved; antheridia 1–4 per bract, the body with irregular, non-tiered cells, the stalk usually conspicuously elongated, usually 2-seriate. Gynoecia on leading shoots, bilateral, with 1–3 subfloral innovations (especially when not fertilized), the bracts leaf-like; bracteole absent (except *Herzogobryum* and *Acrolophozia*). Perianth usually ± included (except *Herzogobryum* and *Acrolophozia*), abbreviated to vestigial (lacking in *Gymnomitrion*), the perianth usually subtended by a ring- or tube-like *Isotachis*-type perigynium that sometimes is bulbous ventrally and then forming a marsupium-precursor.

Seta usually rather short, the capsule often barely exserted, of many cell rows (except *Marsupella* spp. and *Cephalomitrion*). Capsule spherical, the wall 2-, rarely and locally 3-stratose; outer layer of cells never strongly elongated, with one-phase ontogeny, with all but shortest walls with usually strong, radial (nodular) thickenings that occasionally are coalescent; inner layer of cells with radial thickenings that locally to commonly tangentially extend to form incomplete to complete semiannular bands.

Spores finely granulate, 2–2.5× elaters in diam. Elaters weakly tapered on ends, with 2, rarely 3 or 4 spirals.

Type: *Gymnomitrion* Corda, *nom. cons.*

A family with some eight genera, as follows:

1) *Acrolophozia* R.M.Schust., with three species, all Austral;
2) *Apomarsupella* R.M.Schust. has three species, one (*A. africana* (Steph.) R.M.Schust.) that occurs in Chile and in the mountains of Central Africa (cf. Váňa, 2003);
3) *Gymnomitrion* Corda, with 13–15 species (Schuster, 1974a), two occurring in our area, one in Australia, *G. incompletum* (Gottsche) R.M.Schust., one in Chile, *G. concinnatum* (Lightf.) Corda, and one present in South Africa, *G. laceratum* (Steph.) Horik.
4) *Herzogobryum* Grolle, with five Austral species;
5) *Marsupella* Dumort., with 40–45 species, including two that occur in our area;
6) *Nanomarsupella* R.M.Schust., of the northern Andes;
7) *Nothogymnomitrion* R.M.Schust., monotypic, of New Zealand, Tasmania and southern South America, Falkland Islands, South Georgia, Tristan da Cunha;
8) *Prasanthus* Lindb. & Arnell, with only *P. suecicus* (Gottsche) Lindenb. & Arnell of the high-Arctic regions of the Northern Hemisphere.

Schuster (2002a) removed *Stephaniella* Jack and *Stephaniellidium* S.Winkler *ex* Grolle from the *Gymnomitriaceae* and placed them in the family *Stephaniellaceae* (R.M.Schust.) R.M.Schust. *Lophonardia* R.M.Schust., with only *L. caespitosa* R.M.Schust., which was included in the *Gymnomitriaceae* (e.g., Schuster, 2002a), is now considered a synonym of

Lophozia laxifolia (Mont.) Grolle (Gradstein et al., 2001, p. 115; Engel and Gradstein, 2003, p. 764). *Poeltia* Grolle of Nepal was placed as a subgenus of *Marsupella* by Schuster (1996d, 2002a). *Paramomitrion* R.M.Schust. of the northern Andes was placed in the *Gymnomitriaceae* by Schuster (1996d) and Gradstein et al. (2001), but was placed in the *Jungermanniaceae* subfam. *Eremonotoideae* by Schuster (2002a) and that placement is followed here.

Acrolophozia R.M.Schust.

Acrolophozia R.M.Schust., Rev. Bryol. Lichénol. 34: 259. 1966.

Plants firm, loosely prostrate to, with crowding, ascending, pale green to yellowish green to yellowish brown to deep brown, medium, to 950(1250) μm wide. Branching sparse to common, the branches lateral-intercalary; geotropic, microphyllous axes lacking. Stems rather fleshy, light green to weakly brownish, the cortex not or weakly differentiated, in 1(2) layers of thick-walled, chlorophyllose cells; medullary cells leptodermous, the dorsal 3–4 strata a little larger in diameter than ventral strata. Rhizoids few, colorless, scattered. Leaves vertical, strongly, regularly and stiffly laterally spreading, contiguous to rather closely imbricate, transversely oriented, the insertion transverse dorsally, succubous ventrally, the insertion extending dorsally beyond stem midline; leaves oblong to oblong-ovate, concave, bilobed to 0.12–0.45 (2[3]-lobed in *Acrolophozia fuegiana*), the lobes abaxially ± concave to concave-sulcate, loosely folded over each other; lobes acute or ovate-acute, sharp or cuspidate, the margins entire; lamina margins entire, the dorsal not decurrent. Cells thin- or weakly firm-walled, with concave-sided trigones, the median cells to 12–20 μm wide × 17–24 μm long, the basal cells scarcely larger, not elongated; surface conspicuously and coarsely papillose, the papillae close to crowded, guttulate, becoming weakly to only moderately elongated toward leaf base. Oil-bodies (*A. pectinata*) occupying conspicuous portion of cell lumen, hyaline, 2–4(6) per median disc cell, finely papillose. Underleaves lacking the ventral merophytes 1–2 cells broad. Asexual reproduction lacking.

Autoecious. Androecia on leading shoots, rather short lateral-intercalary branches, or gynoecial innovations, terminal but soon becoming intercalary; bracts usually in 4–8 pairs, leaf-like, scarcely smaller than leaves but a little more imbricate, the base at most moderately concave, never strongly ventricose, a dorsal tooth lacking; antheridia 1–2 per bract, the stalk uniseriate. Gynoecia terminal on leading shoots or rather short lateral-intercalary branches issuing from leading shoots; bracts in 2–3 series, grading into leaves, suberect to erect, concave, bifid like leaves; bracteole usually present (?always) as a narrow lobe very broadly connate with 1 bract (the bract then appearing trifid). Perianth closely sheathed by the 2–3 pairs of imbricate bracts that collectively form a ± distinct capitulum, the perianth not or barely exceeding the innermost bracts; perianth distinct and well developed, 1-stratose, not subtended by a perigynium (or with a low ring-like one), ovoid to oblong-ovoid, bluntly 3–6-plicate distally, the sulci shallow except at perianth apex; mouth contracted, crenulate to crenulate-denticulate by moderately elongated, slightly firm-walled, hyaline cells that are free at their apices. Calyptra thin, formed entirely from archegonial venter, with unfertilized archegonia basal.

Seta short, the capsule hardly exserted, with ca. 25–26 rows of outer cells averaging slightly smaller in diameter than the many internal cell rows. Capsule spherical or nearly so, irregularly vertically dehiscing into valves of irregular shape and width, the wall 2-layered; outer layer of cells higher than the inner, irregularly subquadrate to short-rectangular, the longitudinal walls all with 1–2(3) strong but well-isolated nodular thickenings that are typically stalked

and dilated distally (occasional ones extended as obscure tangential spurs), the transverse walls with 0–1(2) similar thickenings; inner layer of cells similar in size and shape, the radial walls with thickenings similar to the outer wall but considerably weaker and more often extended as spurs, rarely extended to form weakly defined, complete semiannular bands (well-formed semiannular bands lacking).

Spores yellow-brown, 10–11 μm in diam., faintly granulate-asperulate, 1.5–1.6× elater diam. Elaters 6–7 μm wide, 3-spiral, the spirals yellow-brown, narrow.

Type: *Acrolophozia pectinata* R.M.Schust.

A genus with three species, all subantarctic in range. *Acrolophozia fuegiana* R.M.Schust. (Schuster, 1968a) is known from South Georgia (Hässel, 1980b), the Falkland Islands (685 m) and Tierra del Fuego (Cerro Garibaldi, ca. 900 m, type). *Acrolophozia sulcata* Hässel (Hässel, 1980b) is endemic to South Georgia, and *A. pectinata* occurs in our area. We agree with the remark by Schuster (2002a, p. 519) that the position of the last species in *Acrolophozia* requires confirmation.

Description adapted and modified from Schuster (2002a).

References: Schuster (1966c, 1996d, 2002a).

Acrolophozia pectinata R.M.Schust.

[Fig. 175: 1, oil-bodies, p. 787]

Acrolophozia pectinata R.M.Schust., Rev. Bryol. Lichénol. 34: 261. *f. 3*. 1966. Type: New Zealand, South Is., Mt. Cook Natl. Park, South Canterbury, Sealy Ra., ca. 500 ft. above Sealy Lakes, 4500–4800 ft., *R. & O. Schuster 49703*.

Plants pale green to golden brown to pale brown (exposed sectors of the shoot). Branching sparse to common, the branches lateral-intercalary, often becoming long and leading shoots. Stems with surface of cortical cells strongly papillose or smooth or nearly so. Leaves rigid, rather fragile, ± spreading, to 900 μm wide × 1175 μm long, leaves oblong to oblong-ovate, concave-canaliculate, with a sharp channel extending from sinus base to leaf base (especially *in situ*), bilobed to 0.35–0.45; lobes markedly abaxially sulcate, with lobe margins + sinus bases strongly reflexed, the lobes rather narrowly to rather broadly acute, the sides gradually tapering, variable in curvature, straight or feebly ± curved to broadly and gently arched, the tip sharp-pointed to cuspidate, the lobes terminating in a single cell or a uniseriate row of 2 subisodiametric cells, the tip cell rounded at the summit, the surface warty from ± spherical papillae; sinus sharp, V-shaped, nearly closed below. Cells tending to be arranged in irregular to ± regular vertical rows and horizontal tiers, thin- or weakly firm-walled, with small, concave-sided trigones, the median cells 12–20 μm wide × 17–24 μm long; cells near leaf bases subisodiametric ranging to 1.1–1.3× longer than wide, up to 18–24 μm wide × 24–30 μm long; surface coarsely papillose, the papillae close to crowded, guttulate, becoming weakly to only moderately elongated toward leaf base, the papillae at leaf base for the most part at most only moderately elliptic in outline, with only isolated, longer, parallel-sided striae. Oil-bodies occupying conspicuous portion of cell lumen, hyaline, 2–4(5) per median disc cell, finely papillose, the spherules slightly protruding beyond membrane, the oil-bodies globose to broadly elliptic.

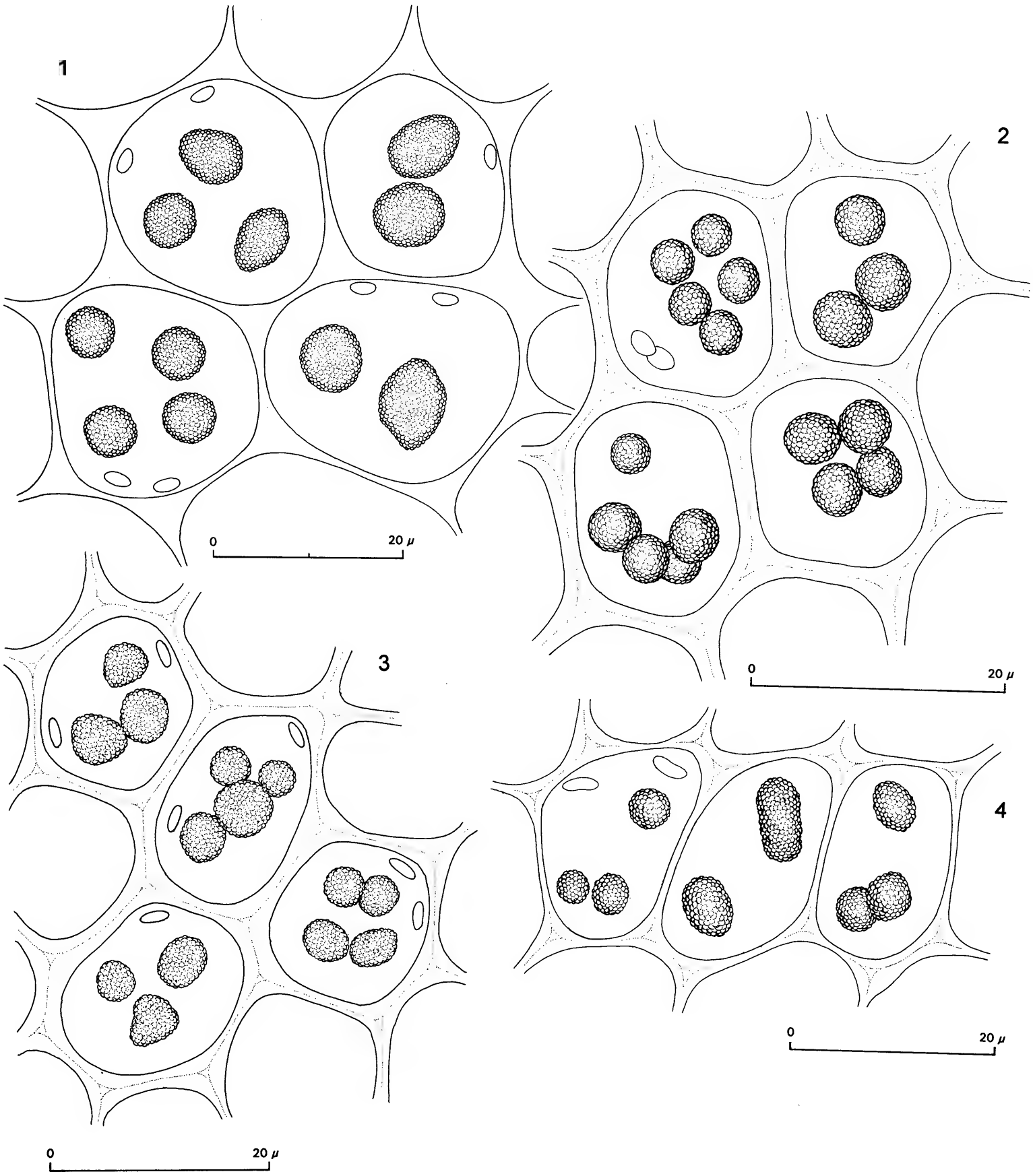

Fig. 175.
Oil-bodies, all with the outline of a few chloroplasts included. 1. *Acrolophozia pectinata* R.M.Schust. Median leaf cells. 2. *Herzogobryum teres* (Carrington & Pearson) Grolle. Median leaf cells. 3. *Nothogymnomitrion erosum* (Carrington & Pearson) R.M.Schust. Median cells of leaf. 4. *Gymnomitrion strictum* (Berggr.) R.M.Schust. Median leaf cells. (Fig. 1, from *Glenny 9414*, New Zealand, South Is., Canterbury EP, Arthur's Pass Natl. Park, Temple Basin; 2, from *Glenny 8868*, New Zealand, South Is., Westland EP, Arthur's Pass Natl. Park, Upper Otira Valley; 3, from *Glenny 9025*, Western Nelson EP, Harwoods Hole; 4, from *Glenny 8867*, New Zealand, South Is., Westland EP, Arthur's Pass Natl. Park, Upper Otira Valley.)

Antheridial bracts bifid to 0.3, with lobe and dorsal margins recurved like the leaves. Gynoecial bracts in 2 pairs, often with decolorate apices, leaf-like, the margins recurved like those of leaves, edentate, the lobes abaxially concave-sulcate, strongly canaliculate, narrowly lanceolate, the lobe apex sharp. Perianth becoming whitish with age, 3–4-plicate.

Distribution and Ecology: Endemic to New Zealand: South Island (1220–1600 m), North Island (1650–1660 m). Known from Fiordland, Westland, Canterbury (Mt. Cook Natl. Park), Sounds–Nelson and Volcanic Plateau EPs.

A plant of alpine areas, occurring on soil over rock in protected niches among boulders or outcrops. For example, at the top of Top of the Bruce (N slope of Mt. Ruapehu, Tongariro Natl. Park, 1660 m), plants occurred over soil under a rock overhang in an area of cliffs and outcrops with scattered alpine plants. It occurs in protected crevices in rock outcrops, but also in more exposed sites with late snowmelt or regular water seepage. For instance, it occurs at Temple Basin (near Arthur's Pass) among shady bluffs with late snow lie in sparse herbfields of *Celmisia*, *Leucogenes grandiceps* and *Ourisia*. Found most commonly with *Andreaea acutifolia* and *Nothogymnomitrion erosum*, but also with *Bartramia papillata*, *Cheilolejeunea campbelliensis*, *Dicranum aucklandicum*, *Diplophyllum domesticum* var. *icari*, *Frullania aterrima*, *Gymnomitrion cuspidatum*, *Herbertus oldfieldianus*, *Hymenophyllum multifidum*, *Notholigotrichum australe*, *Pohlia wahlenbergii*, *Radula sainsburiana* and *Riccardia crassa*.

Comments: The species may be identified by the combination of medium plant size, leaves bifid to 0.35–0.45 by distinctly abaxially sulcate lobes and complete absence of underleaves. The lobe margins and sinus bases are notably strongly reflexed and the lobes gradually taper to a sharp-pointed to cuspidate tip. The leaf surface is strongly papillose, with crowded, close, hemispherical, guttulate papillae. The artificial key on p. 687 (*sub Andrewsianthus*) distinguishes this species from those with a similar appearance.

Shoots are typically relatively short, but occasional populations have plants that are considerably elongate. These are often less pigmented, with pure green shoots at times intermixed. Such plants have crowded, well-developed papillae.

Herzogobryum Grolle

Herzogobryum Grolle, Rev. Bryol. Lichénol. 32: 160. 1964 (1963).
Chondrophyllum Herzog, Rev. Bryol. Lichénol. 21: 46. 1952, *non Chondrophyllum* Kylin, Acta Univ. Lund. N.S. 20(6): 442. 1924 (*Rhodophyta*).

Plants wiry, filiform, often vermiform, often slenderly terete, greenish to greyish green to brownish, small, to 400 μm wide. Branching sparing, the branches usually lateral-intercalary and ?ventral-intercalary; *Frullania*-type branches rare; geotropic microphyllous axes lacking. Stems wiry, rigid, the cortex weakly differentiated, in 1–3 layers of often decolorate, weakly to distinctly firm-walled cells; medullary cells weakly to distinctly firm-walled and with rounded lumina. Rhizoids sparse, scattered, colorless. Leaves suberect or erect-appressed, often somewhat dorsally displaced, densely imbricate, often scale-like at stem base and becoming continuously larger distally, the insertion subtransverse to feebly to distinctly succubous, on a lunate line, the insertion lines interlocking dorsally; leaves unistratose (aside from basal field) or (*Herzogobryum vermiculare*) 2–3-stratose, strongly concave to hemispherical or saucer-shaped, usually ovate to subrotundate to quadrate, unlobed or 0.1–0.2 bilobed; margins erose-denticulate, with ± differentiated cells; surface smooth or delicately striolate toward leaf

base. Oil-bodies relatively large, 1–2 to 2–8 per cell, finely papillose ("finely granular botryoidal," Schuster, 2002a, p. 520). Underleaves lacking or (usually) rudimentary; ventral merophytes vestigial, the insertion lines approximated ventrally. Asexual reproduction absent.

Dioecious. Androecia not distinctly differentiated, eventually intercalary, the bracts in few pairs, leaf-like; antheridia 1 per bract, the stalk 1- or 2-seriate. Gynoecia clavate or subclavate, the bracts gradually larger than leaves, shallowly lobed (even if leaves unlobed); bracteoles present, small or ± large and broad, sometimes approaching bracts in length, free or ± connate with one or both bracts. Perianth well developed, lacking a subtending stem perigynium, usually at least to 0.1–0.2 emergent, lophozioid in form, ovoid to ellipsoidal, strongly pluriplicate, contracted toward the plurilobulate mouth, the lobules crenulate-denticulate or (*Herzogobryum vermiculare*) fimbriolate, the cells at mouth barely free laterally grading to entirely so, rounded at the summit. Calyptra thin, with sterile archegonia only near base.

Seta massive. Capsule spherical, the wall 2-stratose; outer layer of cells higher than inner cells, with strong nodular thickenings, especially on all longitudinal walls; inner layer of cells narrower, with numerous, relatively weak nodular thickenings, the thickenings at times tangentially extended as spurs, without semiannular bands.

Spores finely granulate to nearly smooth, 9–14 μm in diam., ca. 1.2–1.5 diam. of elaters. Elaters bispiral, 7–10 μm wide.

Type: *Herzogobryum cucullatum* (Herzog) Grolle (≡ *Chondrophyllum cucullatum* Herzog)

A genus of five species, all cool to cold south temperate–subantarctic in range, and several with a circum-subantarctic distribution. All occur in New Zealand except *Herzogobryum molle* Grolle, which is known from Tristan da Cunha, Tierra del Fuego and the Valdivian zone in Chile (Cerro Tesoro Massiv, Prov. Aisen) as well as in Argentina (Parque Natl. Nahuelhuapi).

Treatment of genus adapted and modified from Grolle (1966b) and Schuster (1996d, 2002a).

References: Grolle (1966b), Schuster (1996d, 2002a).

Key to Species

1a. Marginal leaf cells delicate, with walls thinner than the ± firm-walled and/or collenchymatous intramarginal cells 2
  2a. Leaves unistratose (aside from a basal field), typically a little succubous in insertion, on lax shoots unlobed or 0.15–0.2 bilobed 3
    3a. Cells, except in margin, equally thick-walled, 9–13 × 10–18 μm; shoots thread-like, typically 100–140(150) μm wide with leaves; leaves ca. 18–20 cells wide, emarginate but scarcely bilobed, or at most, bilobed to 0.25 4
      4a. Plants light to grey green (except gynoecia brownish red); leaves ca. 0.15–0.25 bilobed, the lobes apiculate; leaves when dry not folded, ± weakly abaxially convex . . . . . *H. filiforme* (p. 790)
      4b. Plants piceous; leaves obscurely emarginate, when dry the distal portions folded together, the leaves obscurely keeled above . . . . . *H. atrocapillum* (p. 791)

3b. Cells thin- to firm-walled with trigones minute to small, 15–25 × 15–26 μm medially; shoots over 150 μm wide; leaves over 20 cells broad, unlobed. Leaves not folded or keeled in drying, with lamina evenly convex; stems with cortex ± undifferentiated, the cells of ± the same size; antheridial stalk 2-seriate . . . . . *H. teres* (p. 792)

2b. Leaves with lamina, exclusive of the hyaline border, 2–3-stratose, remote, inserted on an arcuate, shallowly U-shaped line; leaves unlobed . . . . . *H. vermiculare* (p. 794)

1b. Marginal leaf cells in 1–2 rows, hyaline, exceedingly thick-walled, the free walls extended as knob-like protrusions or denticulations . . . . . [*Nothogymnomitrion*; p. 795]

Herzogobryum filiforme R.M.Schust.

Herzogobryum filiforme R.M.Schust., Phytologia 45: 422. 1980. Type: New Zealand, South Is., Mt. Cook Natl. Park, above Sealy Lakes, *Schuster 67-4417*.

Plants wiry, very slender, terete, light green to light grey green, except for the brownish red–tinged gynoecia (inner bracts), the sterile axes only 100–130(150) μm in diam., the shoots elongated and arcuate, rather subacutely tipped distally, for the most part simple and hardly branched. Stems whitish green, very slender. Leaves dense, erect-appressed, scale-like and very small, hardly discernible on the leafy shoots, unistratose throughout, rather concave, when flattened quadrate-rotundate to rotundate-ovate, widest usually just below middle and here under 19 cells broad, ca. 180–200 μm wide × 190–225 μm long, ca. 0.15–0.25 bifid; lobes as wide or wider than long, broad acute, apiculate with a single hyaline, often elongated cell; sinus V-shaped to broadly rectangulate. Leaves light green, rather hyaline, with a border of echlorophyllose, hyaline cells; marginal cells thin- or weakly thick-walled, ± elongated at nearly right angles to leaf margins, typically 9–14 μm wide × 16–30(32) μm long, triangular to finger-like, free for ca. 0.25–0.75 their length, the free ends projecting as narrowed, distally rounded, smooth crenulations; intramarginal, subapical, median and basal cells almost uniformly similar in size, short-oblong to polygonal, equally thick-walled (the walls much thicker than in marginal cells), 9–17 × (10)12–18 μm; basal cells to 10–13 × 16–21 μm; surface everywhere smooth. Underleaves absent. Asexual reproduction absent. Fungal partner absent.

Dioecious. Androecia unknown. Gynoecia terminal on stem or branches, abruptly rather clavate-subcapitate, ± frontally compressed, becoming gradually larger distally, consisting of 4–6 pairs of tightly imbricate bifid bracts; bracts of innermost series 0.35–0.45(0.5) bifid, the lobes narrow and long-acute to subacuminate, of thick-walled, brownish to reddish castaneous cells, the lobe margins irregularly crenulate to denticulate with often elongated, tapered to pointed, triangular to diamond-shaped cells, the bracts without hyaline margins. Perianth (only juvenile known) with mouth hyaline, the margin like those of leaves.

Sporophyte unknown.

Distribution and Ecology: Endemic to New Zealand: South Island (870–1220 m). Known only from Canterbury and Westland EPs. The type is from the alpine tussock grassland zone above Sealy Lakes (Mt. Cook Natl. Park) admixed with *Acrolophozia pectinata* and *Gymnomitrion*. Schuster (1996d) also cited a specimen from the upper Otira River (Arthur's Pass Natl. Park, Westland), a *J. Child* collection found at 1220 m on moist rocks near the snowline,

occurring with *Acrolophozia pectinata*, *Andreaea acutifolia*, *Gymnomitrion cuspidatum*, *Diplophyllum dioicum* and *Riccardia crassa* (CHR 427297). Also occurring on rock in the vicinity of Wakefield Falls in the upper reaches of a *Podocarpus hallii* forest (east-facing slope of Mt. Wakefield, Mt. Cook Natl. Park, 870 m).

Comments: Plants are wiry and notably slender with sterile shoots only 100–130 μm wide, and are light to greyish green, lacking the reddish pigmentation typically found in our other *Herzogobryum* species. The leaves are bilobed to ca. 0.15–0.25, and are at most only 18–20 cells wide at their widest point. The lobes are as wide or wider than long, apiculate and terminate in a single cell that is often elongated.

Herzogobryum atrocapillum (Hook.f. & Taylor) Grolle

Gymnomitrium atrocapillum Hook.f. & Taylor *in* Taylor, London J. Bot. 5: 258. 1846. *Jungermannia atrocapilla* (Hook.f. & Taylor) Taylor & Hook.f. *in* Hook.f., Bot. Antarc. Voy. 2: 423. 1847. *Cesia atrocapilla* (Hook.f. & Taylor) Mitt., Phil. Trans. Roy. Soc. London 168: 43. 1879. *Cesiusa atrocapilla* (Hook.f. & Taylor) Kuntze, Revis. Gen. Pl. 834. 1891. *Acolea atrocapillum* (Hook.f. & Taylor) Steph., Sp. Hepat. 2: 4. 1901. *Herzogobryum atrocapillum* (Hook.f. & Taylor) Grolle, Oesterr. Bot. Z. 113: 228. 1966. Type: Kerguelen, Foul Haven, 200 m, *Hooker*.

Gymnomitrium marionense S.W.Arnell, Svensk Bot. Tidskr. 47: 415. 1953. Type: Marion Is., *Rand 3788*.

Plants thread-like, hair-like, nearly terete, vermiform (due to uniformly appressed leaves), creeping but lateral branches (often ♂ or ♀) often ascending, usually deep red-brown to piceous (but with hyaline margins of leaves), even in sheltered sites rarely green, the intramarginal sector of leaves and the median sector of perianths with red-brown or brownish pigmentation, the leafy shoots very narrow, 125–145 μm in diam., occasionally 160–165(170) μm in diam., with the imbricate and appressed leaves so closely applied as to be almost indistinguishable, but when dry the shoots obscurely laterally keeled due to the somewhat keeled leaves (usually perceptible only on cleared shoot apices). Branching freely occurring, irregular, the branches (evidently) all lateral-intercalary; geotropic, microphyllous axes lacking. Stems rigid, thick for shoot size, the cortical cells firm-walled, feebly differentiated, in 1.5–2 layers of thick-walled cells slightly larger in average diameter than the thick-walled, colorless medullary cells. Rhizoids very few, scattered, limited to older shoot sectors, colorless. Leaves in lower shoot sectors scale-like, often becoming bleached, those above densely erect-appressed (the entire leaf tightly appressed), the stem nowhere visible in dorsal aspect, the leaves almost transversely to weakly succubously inserted, the insertion lines extended across stem midline (the lateral merophytes interlocking), the leaves in basal two thirds strongly concave and with a rounded, ± gutter-like "keel" (in dried state the leaves contracted at the apex and ± keeled); leaves broadly ovate, impossible to flatten without tearing, emarginate to bilobed to 0.15–0.2, the distal portion of leaves tending to be loosely folded, obscurely keeled, sometimes connivent and somewhat dorsally secund (thus, *in situ*, the leaves collectively forming a ± flat dorsal surface of the shoot, the shoot strongly convex on the ventral surface only); lobes short, triangular, their margins often incurved, largely decolorate and leaf margins proximal to lobes hyaline-margined, the hyaline marginal cells thin-walled, often erose with age, forming prominent denticulations. Leaves with marginal cells differentiated, thin-walled, bleached and empty, forming a border 1–2 cells wide, even on young leaves, the marginal cells variable, but often radially somewhat elongated (and 9–11 × 15–22 μm), their ends narrowed, projecting and

lending the margins crenulate, rounded at the summit; lamina cells conspicuously and evenly thick-walled, lacking trigones, the lumina angular-rounded, the cells small, 10–15 × 11–18 μm, the cells toward leaf base somewhat larger, to 13–16 × 16–20 μm; surface smooth. Underleaves lacking, the ventral merophytes very narrow.

Dioecious. Androecia often on lateral branches of limited length, terminal but becoming intercalary, the shoots often repeatedly androecial; bracts mostly in 2–4 pairs (the leaves below the androecia gradually larger and grading into the bracts), dorsally assurgent, slightly saccate, strongly ventricose, the apices contracted and appearing somewhat beaked; antheridia solitary. Gynoecia terminal on mostly lateral branches of varying length, if fertilized never innovating (but often with a lateral-intercalary branch from lower down on the gynoecial axis); bracts much larger than leaves, together with the perianth forming a clavate, abruptly enlarged, capitulum 3–3.5× wider than sterile shoot sectors, bracts broadly ovate or ovate-deltoid, bilobed to 0.2–0.3, when young hyaline-margined but at maturity becoming erose-margined, the margins strongly serrulate-denticulate with elongated, in part finger-like cells; bracteole lacking (or ?vestigial). Perianth long-ovoid, widest in basal third and gradually narrowed, green basally, brown pigmented in median third, contracted at mouth, the apical 0.2–0.35 bleached, strongly pluriplicate, the mouth cells fragile and easily broken, mostly in broken condition.

Sporophyte not seen.

Distribution and Ecology: Circumsubantarctic; New Zealand: South Island; Heard Island (Bergstrom and Selkirk, 1997), Kerguelen Island, Crozet Island, Marion Island, Prince Edward Island, Antarctica (Bouvetoya, South Orkney Islands; cf. Bednarek-Ochyra et al., 2000). In New Zealand known only from the Scotts Track station (Arthur's Pass Natl. Park, South Island), reported by Schuster (1996d).

Comments: Plants are thread-like (typically at most 140 μm wide), and due to the uniformly appressed leaves, are markedly vermiform. The leaves are imbricate and so closely appressed as to be nearly indistinguishable; when dry, the distal portions are folded together lending the leaves obscurely keeled above. The leaves are emarginate to short-bilobed, 18–20 cells wide, with intramarginal cells equally thick-walled and only 9–13 × 10–18 μm.

Herzogobryum teres (Carrington & Pearson) Grolle

[Plate 16A, B; Fig. 175: 2, oil-bodies, p. 787]

Jungermannia teres Carrington & Pearson, Pap. & Proc. Roy. Soc. Tasmania 1887: 9. *pl. 7, f. 1–16*. 1888 ("*Jungermania*"). *Jamesoniella teres* (Carrington & Pearson) Steph., Sp. Hepat. 2: 100. 1901. *Herzogobryum teres* (Carrington & Pearson) Grolle, Oesterr. Bot. Z. 113: 223. 1966. Lectotype (cf. Grolle, 1966b): Tasmania, Mt. Wellington, *Bastow*.

Acolea magellanica C.Massal. & Steph. *in* C.Massal., Atti Reale Ist. Veneto Sci. Lett. Art. 87: 237. *pl. 3: 5–7*. 1928. Type: Argentina, Isla de los Estados, Penguin Rookery, *Spegazzini*.

Jamesoniella inflexo-limbata Herzog, Trans. & Proc. Roy. Soc. New Zealand 68: 41. 1938. Type: New Zealand, Mt. Tongariro, 12 Jan. 1933, *Moore 130*.

Plants wiry, but rather fleshy and rigid, terete, julaceous, worm-like, somewhat nitid, green, at least upper surface of shoots, occasionally dull or rusty red or yellow-brown (but leaf margins decolorate), the shoots relatively stout, to 410 μm wide, the upper parts evenly leafy. Branching mostly lateral-intercalary, occasionally ?ventral-intercalary. Stems fleshy, colorless, stiff and wiry, the cells of ± the same size, the outer 1.5–3 cell layers pale and thin-walled; medullary

cells slightly to distinctly thick-walled. Rhizoids scarce, scattered, colorless. Leaves erect, loosely appressed, mostly subcontiguous to weakly to moderately imbricate, the insertion feebly to distinctly succubous, the insertion line broad, basiscopically arched, bowed (insertion both dorsally and ventrally obliquely arched toward shoot apex), the insertion lines extending considerably beyond stem midline; leaves unistratose (or in larger phases with a 2-stratose median-basal field), concave, saucer-shaped, orbicular-ovate, wider than long when flattened, (22)24–40 cells wide at widest point, to 375–400 × 480–515 μm, broad-based and clasping the stem, unlobed; marginal cells differentiated into a hyaline, empty, incurved (especially apically) border (1)2–4 cells broad, the outermost row of radially or obliquely elongated cells (10–15 × 25–32 μm) that are relatively thin-walled and forming a crenulate, conspicuous border, often breaking down with age, the margin then erose; intramarginal cells thin- to clearly thick-walled, trigones minute to small and concave-sided or less often medium and straight-sided, the cells 15–25 × 15–26(29) μm medially and subapically; surface typically minutely papillose–short-striate, the striae oriented perpendicular to the cell walls, the surface rarely rather long-striate with striae oriented strictly longitudinal, the surface rarely smooth. Oil-bodies in intramarginal cells of leaf, absent from hyaline marginal cells which also lack cell contents, the oil-bodies occupying a small portion of the cell volume, pale smokey grey, 2–5 per cell, finely papillose, subglobose to irregularly elliptic, 3.8–5.3 × 6.7–7.7 μm, globose ones 4.8–5.8 μm in diam. Underleaves frequently developed, lanceolate, small to rather large, to 60 μm wide × 200 μm long, united for most of their length with an adjacent lateral leaf, hyaline, crenulate-margined. Fungal partner absent.

Dioecious. Androecia terminal but becoming intercalary; bracts in few pairs, lacking a lobule, slightly ventricose, the dorsal base slightly broadened and incurved; antheridia single, the stalk 2-seriate. Gynoecia terminal on abbreviated or long branches; bracts in several tightly imbricate series, those of innermost series larger than leaves, shallowly 2-lobed and irregularly and sparsely coarse-dentate to lobulate, with recurved margins, at least in sinuses; bracteole free, large, broad, rarely approaching bracts in size, usually pointed or bilobed or lobulate. Perianth long-emergent, *Lophozia*-like, ovate, strongly pluriplicate, apically strongly and sometimes rather abruptly contracted, not compressed, the mouth plurilobulate, the lobules denticulate by rectangular cells; perianth 1-stratose in the densely pluriplicate distal sectors, becoming 3–4(5)-stratose basally, the cells at and below mouth rectangular. Calyptra 2-layered to above its middle, becoming 3–4-layered toward middle and 4–5-layered toward base.

Sporophyte unknown.

Distribution and Ecology: "A circumsubantarctic species and the commonest and most widespread within the genus" (Bednarek-Ochyra et al., 2000, p. 139); New Zealand: Campbell Island, Stewart Island (600–720 m), South Island (1010–1970 m), North Island (1080–2300 m); Australia: Tasmania; Antarctica (Bouvetoya, South Orkney Islands, South Shetland Islands); South Georgia; Falkland Islands; southern South America (Tierra del Fuego); Tristan da Cunha; Gough Island; Marion Island. In New Zealand known from Fiordland, Otago, Westland, Canterbury, Sounds–Nelson, Taranaki (Mt. Taranaki), Volcanic Plateau (Tongariro Natl. Park) and Gisborne (Mt. Hikurangi) EPs.

The most frequent of our *Herzogobryum* species, typically associated with alpine areas and in these sites occurring on exposed faces of boulders and outcrops, in rock crevices or deep under protective rock overhangs or between boulders where a sizeably, often thick layer of soil has accumulated and on moist cliff faces. In such sites, it occurs with *Acrolophozia pectinata*, *Andreaea acutifolia*, *Andrewsianthus cuspidatus*, *Arthroraphis alpina*, *Dicranoweisia*

antarctica, *Jamesoniella colorata*, *Nothogymnomitrion erosum*, *Notholigotrichum australe*, *Racomitrium crispulum* and *Rhacocarpus purpurascens*, more rarely, on Stewart Island, with *Cryptochila acinacifolia*, and in Otago with *Ptilidium ciliare*. Occasionally found in the penalpine zone, for example at 1240 m in an exposed stream valley through penalpine scrub of *Halocarpus bidwillii*, *Ozothamnus leptophyllus* and *Phyllocladus alpinus* (Taranaki Falls Track, Tongariro Natl. Park). On Stewart Island occurring on an exposed ledge of a large rock outcrop at 600–690 m in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* from 0.5 m to 2 m tall and significant areas of exposed rock (Mt. Rakeahua summit area). Plants vary from semi-isolated shoots to formation of loose to tight mats; plants exceptionally may form tight compact small mounds.

Comments: This is the largest New Zealand *Herzogobryum* species. Leaves normally are 24–40 cells wide at widest point, unlobed, with cells 15–25 × 15–26 μm medially and cell walls thin- to firm-walled with trigones minute to small and concave-sided. The stem cortex is ± undifferentiated with the cells of ± the same size throughout. Plants from exposed sites develop notable rust-red pigments except for the decolorate, bleached, marginal sectors.

Small phases of the species may have leaves only 17–21 cells wide and therefore may cause confusion. However, such plants have unlobed leaves, with median leaf cells 17–24 μm wide × 20–23 μm long. Such populations nevertheless may produce sporophytes.

Herzogobryum vermiculare (Schiffn.) Grolle

Gymnomitrium vermiculare Schiffn. *in* Naumann, Forschungsr. Gazelle 4(4): 2. *pl. 1, f. 9, 10*. 1890. *Herzogobryum vermiculare* (Schiffn.) Grolle, J. Hattori Bot. Lab. 28: 103. 1965. Type: Kerguelen, Successful Harbor, 1874, *Naumann*.

Chondrophyllum cucullatum Herzog, Rev. Bryol. Lichénol. 21: 46. *f. 1–2*. 1952. *Herzogobryum cucullatum* (Herzog) Grolle, Rev. Bryol. Lichénol. 32: 160. 1963. Type: Chile, Prov. Aisén, Cerro Tesoro, ca. 1000 m, 13 Feb. 1940, *Schwabe 39c p. p.*

Plants fleshy (rather than wiry), rather rigid when dry, greenish throughout or, more often, brownish green to brick-red on leaves within the hyaline border, the plants relatively vigorous, the shoots (including leaves) 625–685 μm wide, rarely larger, 10–20 mm long or more, remotely to loosely catenulate-leaved. Branching rather common but irregular, the branches mostly lateral-intercalary from near ventral end of leaf axils; *Frullania*-type branches sometimes present; flagelliform, microphyllous branches lacking. Stems rigid and stout, the cortex in 1 layer of rather thin-walled, tangentially flattened cells surrounding 2–3 strata of progressively firmer-walled intracortical cells that are subisodiametric in cross section; medullary cells strongly thick-walled, with reduced lumina (in cross sections often angular to substellate). Rhizoids rare or absent. Leaves erect to suberect, appressed to stem, the base clasping the stem, the leaves remote to contiguous (the stem always ± exposed in dorsal view), the insertion forming an acroscopically arched line; leaves usually (2)3-stratose except for apices and marginal sectors, strongly cochleariform-concave (in cross section lunate), subrotundate but (because of the strongly concave form) impossible to flatten without tearing, undivided, the margins indistinctly crenulate. Cells of leaves (epidermal, abaxial) ± irregularly polygonal to short-oblong, somewhat thick-walled, trigones lacking or distinct and small, the median cells 14–20 × (16)18–24(26) μm, the cells ± similar in size almost throughout leaf; surface smooth. Underleaves absent. Fungal partner absent.

Dioecious. Androecia compactly spicate, the bracts in 3–4 to many pairs, contiguous to closely imbricate (the hyaline marginal sectors ± closely appressed to bracts immediately above), strongly concave, orbicular, entire; antheridia monandrous, the stalk 2-seriate. Gynoecia terminal on leading shoots or ± elongated lateral-intercalary branches, the bracts in 2–3 closely imbricate pairs, grading below into leaves, the inner bracts of innermost series often strongly dimorphic: one 3–4-lobed or lobulate, very broadly ovate and wider than long, the other usually shallowly lobed or lobulate at apex and ovate; bracteole distinct, free, rather large, lanceolate. Perianth and bracts forming a compact, mostly ovoid to obovate capitulum, the bracts closely sheathing perianth base, but distal half or more of perianth emergent, the perianth terete below, conspicuously plicate above, not compressed above, contracted to a rather small mouth, the mouth shallowly lobulate, the lobules fimbriolate by processes terminating in a uniseriate row of 2–4 cells; perianth mostly 6–7-stratose below, remaining 2(3)-stratose to within 0.2 of apex.

Seta massive, of numerous rows. Capsule spherical, the wall rather firm (at least locally 3-stratose), the valves brittle and usually fragmenting after spore discharge; outer layer of cells mostly oblong, with very strong, often opposed, nodular thickenings of longer walls, the transverse walls frequently with a pair of such thickenings; inner layer of cells less regular, often narrowly oblong, variable, with much weaker nodular thickenings.

Spores 14–18 μm in diam., minutely granulate. Elaters short and slender, hardly to quite tortuous, with blunt ends, 8–9 μm wide, with 2 or 3 spirals, the spirals often rather lax to close, narrow, under 2 μm wide.

Distribution and Ecology: Mainly subantarctic in distribution; New Zealand: South Island (1650 m), North Island (1790 m); South Georgia, Falkland Islands, southern South America only at ca. 1000 m in the Valdivian region, Kerguelen Island, Marion Island, Prince Edward Island (Schuster, 1996d) (also cf. Engel, 1990a).

A species known from a few scattered loci. In the alpine zone immediately below the summit of Avalanche Peak (Arthur's Pass Natl. Park, 1650 m) occurring admixed with *Acrolophozia pectinata* and *Nothogymnomitrion erosum* in a protected niche of a rock outcrop. Also on the northern slope of Mt. Ruapehu (S of Top of the Bruce, Tongariro Natl. Park, 1790 m) on soil under a ledge of an outcrop in an area of cliffs and outcrops with scattered alpine plants.

Comments: Plants of this species *in situ* and even when dry may be distinguished from other members of the genus and from *Nothogymnomitrion* (both of which are commonly admixed) by the smaller plant size coupled with the remotely to loosely catenulate-leaved shoots. Leaves are unlobed and 2–3-stratose (exclusive of the hyaline border); all other members of the genus have unistratose leaves (aside from a basal field at times present in some species).

Nothogymnomitrion R.M.Schust.

Nothogymnomitrion R.M.Schust., J. Hattori Bot. Lab. 80: 43. 1996.

Plants often in dense, unordered, compact mats, wiry, rigid, nearly terete, vermiform, creeping, erect with crowding, plagiotropic, greenish to golden brown to red-brown. Branching common but irregular, the branches lateral-intercalary, from median sector of axil or from the ventral or sometimes dorsal end of the axil; branches of 2 types: normal and leafy, and stoloniform, the microphyllous branches issuing from lower ends of leafy axes, creeping, with rudi-

mentary 2-ranked leaves and copious rhizoids. Stems rather thick and rigid, striolate in surface view, the cortex very weakly differentiated, in a single layer of slightly larger, firm-walled cells with ± bulging free walls; medullary cells firm-walled, clearly thickened at the angles. Rhizoids colorless, few and scattered on ventral side of normal leafy axes, abundant on stolons and from all sides of axis. Leaves stiffly suberect and weakly laterally spreading, faintly dorsally assurgent, closely and densely imbricate, the insertion subtransverse, shallowly U-shaped, the insertion lines interlocking dorsally for 2–3 or more cell rows (thus lateral merophytes clearly interlocking in a zigzag manner); leaves unistratose, strongly adaxially concave, broadly ovate-deltoid or rounded-deltoid, 270–580 μm wide × 260–500 μm long, usually as wide as long, narrowed to summit, the expanded bases closely investing the stem; apex shallowly emarginate to bidentate-bilobulate, the lobes then often barely perceptible; sinus shallow to vestigial; margins flat, the marginal cells differentiated into border of hyaline, empty, thick-walled cells in 1–2(3) rows, the marginal row mostly elongated radially, ca. 7–13 × 18–36 μm, the cells typically free distally for only 0.5 or less, with the free ends projecting as irregular, extremely thick-walled, notably irregular "knobs" or finger-like, solid projections, the thickened tip at times equaling or exceeding the length of the cell lumen, the margins thus irregularly crenulate-denticulate; intramarginal cells chlorophyllose, in ± regular vertical rows, the cells in 2–several rows at the perimeter (especially in distal sector of leaf) usually pigmented, notably thick-walled, with guttulate lumina, the remaining leaf cells often devoid of strong pigmentation, with progressively thinner walls but rounded at angles, trigones lacking or small and concave-sided to, less often, medium and straight-sided; median cells 11–19 μm wide × 13–22 μm long; basal cells usually thinner-walled, 14–17 × 16–20 μm; surface conspicuously papillose, the papillae in lower parts of leaf wart-like. Oil-bodies occupying a moderate portion of cell, pale smokey grey, hyaline, (1)2–4 per middle of lamina, obscurely coarsely papillose, the spherules not bulging beyond membrane, the oil-bodies globose to subglobose, 2.5–5 μm in diam.; oil-bodies at leaf base 4–7 per cell, at leaf margins 2–3 per cell. Underleaves lacking.

Autoecious. Androecia on leading leafy shoots or ± elongated branches, terminal but becoming intercalary, the shoots sometimes repeatedly androecial, compactly spicate; bracts leaf-like but larger, more spreading and more strongly concave (the androecia thus appearing tumid), the dorsal margin without lobule, but with dorsal margin incurved and ampliate; antheridia 2 per bract, the stalk unistratose but with local bistratose areas, particularly toward base. Gynoecia terminal on leafy axes or branches of variable length, completely lacking a subtending perigynium; bracts in several, progressively larger series (and becoming several times the size of stem leaves), closely imbricate, those of innermost series very variable, symmetrically ovate to ovate-deltoid, short-bilobed, with margins as in leaves but often even more coarsely crenulate-denticulate, the projecting thick-walled hyaline cells sometimes recurved; bracteole always present, rather large, rarely wholly free, usually connate on one or both sides with the bracts (sometimes so broadly so on one side that a 3-lobed bract is simulated). Perianth well developed, not or barely exceeding the innermost bracts, when immature ± strongly laterally compressed, at maturity the mouth remaining perceptibly laterally compressed toward the mouth, proximally inflated, ovate, with a narrowed base; mouth narrowed, shallowly bilabiate, irregularly crenulate-denticulate, with maturation soon becoming erose; perianth cells similar to leaf cells, quadrangular to short-rectangular, slightly thin-walled. Calyptra with unfertilized archegonia at or near base.

Seta very short, usually not protruding capsule beyond bracts, with 22–24 rows of outer cells surrounding an inner core of ca. 30–32 rows, the outer cells not larger than the internal

cells. Capsule subspherical, the wall ca. 24 μm thick, 2-stratose, the outer ca. 2× the inner in thickness; outer layer of cells with strong, nodular thickenings that are often stalked and dilated distally, sporadically extending as weak semiannular bands, the transverse walls also with nodular thickenings; inner layer of cells with nodular thickenings, occasional ones extended as tangential spurs, a few as weak semiannular bands.

Spores brown, 10–14 μm in diam., appearing finely punctate, the spores ± equal to elater diam. Elaters 9–11 μm wide, the tips always rounded, the elaters 3-spiral throughout or at least medially and bispiral toward the ends, the spirals narrow, 1.6–2 μm wide.

Type: *Nothogymnomitrion erosum* (Carrington & Pearson) R.M.Schust. (≡ *Cesia erosa* Carrington & Pearson)

A monotypic genus, with only the subantarctic *Nothogymnomitrion erosum*. Description adapted and modified from Schuster (1996d).

References: Grolle (1966b); Schuster (1996d, 2002a).

Nothogymnomitrion erosum (Carrington & Pearson) R.M.Schust.

[Plate 16C, D, F; Fig. 175: 3, oil-bodies, p. 787]

Cesia erosa Carrington & Pearson, Pap. & Proc. Roy. Soc. Tasmania 1887: 8. *pl. 6, f. 1–19*. 1888. *Gymnomitrium erosa* (Carrington & Pearson) Bastow, Pap. & Proc. Roy. Soc. Tasmania 1887: 244. 1888 ("*erosa*"). *Herzogobryum erosum* (Carrington & Pearson) Grolle, Oesterr. Bot. Z. 113: 231. 1966. *Nothogymnomitrion erosum* (Carrington & Pearson) R.M.Schust., J. Hattori Bot. Lab. 80: 44. 1996. Type: Tasmania, Mt. Wellington, 1 Jan. 1886, *Bastow 284*.

Cesia stygia var. *denticulata* Berggr., On New Zealand Hepat. 4. *f. 4*. 1898. *Acolea denticulata* (Berggr.) Steph., Sp. Hepat. 2: 4. 1901. *Gymnomitrium denticulatum* (Berggr.) Müll.Frib., Rev. Bryol. Lichénol. 20: 176–177. 1951. Lectotype (*fide* Grolle, 1966b): New Zealand, South Is., Kelly's Hill, 1200 m, Feb. 1874, *Berggren 2870*.

For description see the genus.

Distribution and Ecology: Mainly subantarctic in distribution; New Zealand: Campbell Island (570 m), Auckland Islands (170–560 m), Stewart Island (600–690 m), South Island ([695]1010–2130 m), North Island (1240–1700 m); Australia: Tasmania; South Georgia, Falkland Islands (Engel, 1990a); Tierra del Fuego: Isla de los Estados; Brunswick Peninsula, southern Patagonian Channels; Tristan da Cunha. In New Zealand known from Fiordland, Otago, Westland, Canterbury, Marlborough (Tapuae o Unuku), Sounds–Nelson, Southern North Island (Tararua Ra.), Taranaki, Volcanic Plateau and Gisborne (Mt. Hikurangi) EPs.

This species is a common penalpine–alpine plant and is more frequently in the South Island. In the North Island it is associated with volcanic areas, occurring on Mt. Taranaki (Schuster, 1996d) and the central volcanic region in Tongariro Natl. Park. It occurs on rock walls, cliff faces and ledges of outcrops, mostly where a thin soil layer has accumulated, as well as on boulders, frequently on their exposed faces and often where some soil has accumulated. In the alpine zone also on ice-scoured slopes as well as bare soil of steep slopes below cliffs, sometimes on wet rock faces or in snowmelt streams, e.g., on Mt. Burns (Fiordland) where it occurs with *Pachyglossa tenacifolia*. In such alpine habitats it occurs with *Acrolophozia pectinata*, *Andreaea acuminata*, *A. acutifolia*, *Conostomum pusillum*, *Dicranum auck-*

landicum, *Gymnomitrion cuspidatum*, *Herzogobryum teres*, *Jamesoniella colorata*, *Lepidozia obtusiloba*, *Racomitrium striatipilum*, *Rhacocarpus purpurascens*, *Solorina crocea* and *Usnea contexta*. On the summit of Mt. Rakeahua (Stewart Island, 600–690 m), occurring on the sheltered top of a rock face of a large rock outcrop in mosaic communities of penalpine cushion vegetation, herbfields, *Chionochloa*, prostrate *Leptospermum scoparium*, *Olearia colensoi* 0.5–2 m tall and significant areas of exposed rock. This species is able to tolerate xeric conditions perhaps better than any other alpine hepatic. On exposed boulders, for example, it forms a crust with a few species of mosses. It also commonly occurs on steep slopes over exposed soil and stones, there also forming an inconspicuous crust.

Rarely associated with forests, e.g., found on the face of a huge boulder near Lake Marion (Fiordland Natl. Park, 695 m) at the edge of a rather open forest dominated by *Nothofagus menziesii*.

Comments: This species may be readily identified by the marginal row of leaf cells, which is hyaline, exceedingly thick-walled, with their free walls projecting as irregular, extremely thick-walled, solid, notably irregular "knobs." The thickened tips at times equal or exceed the length of the cell lumen. It is more common than *Herzogobryum teres* and is usually distinguishable from that species by the leaves being more imbricate and by a dirty golden brown color rather than a crimson tinting characteristic of *H. teres*.

Marsupella Dumort.

Marsupella Dumort., Commentat. Bot. 114. 1822.

Plants firm but usually not rigid, typically erect, at times loosely procumbent, rarely forming cushions, light or deep green to usually brownish or reddish, or purplish red or piceous to black, minute to robust. Branching sparing, usually from lower, smaller-leaved sectors of leafy axes; branches all lateral-intercalary, from middle or ventral end of leaf axil, of 2 types: phototropic and soon becoming larger-leaved, and geotropic, microphyllous and forming stoloniform, root-like axes. Rhizoids lacking from sectors with mature leaves, usually abundant on geotropic axes. Leaves vertical, usually erect-spreading to stiffly, pectinately spreading (in a few taxa scale-like and erect or sheathing), distant to imbricate (but with stem at least in part exposed), transversely oriented, the insertion transverse in dorsal half, the leaf insertions crossing the stem midline dorsally (except subg. *Stolonicaulon*), the leaves mostly somewhat concave to canaliculate, usually bilobed to 0.15–0.45 (rarely unlobed); lobes usually equal, triangular, blunt or rounded to sharp, entire; marginal cells of lobes and lamina never differentiated, chlorophyllose like others, never decolorate, never forming crenulations or denticulations. Cells with conspicuous, often coarse trigones, the cells usually small, in lobes 8–18 μm, in median sector of lamina 8–15 × 12–22 μm; surface smooth. Oil-bodies (Schuster, 2002a) 2–3(4) per cell, large, finely granular, mostly ovoid or oval. Underleaves completely lacking, the leaf insertions approaching the ventral stem midline.

Dioecious, rarely (but in both of our species) paroecious. Androecia terminal or becoming intercalary, the bracts in 4–12 pairs, not reduced in size, the base strongly ventricose, saccate; antheridia 1–6 per bract, the stalk 1–2-seriate. Gynoecial bracts in (1)2–3 increasingly larger series, the innermost bracts less deeply divided than leaves, ± erect, arising from a ring- or tube-like, fleshy stem-perigynium; bracteoles completely lacking. Perianth short, included within (and ± hidden by) the uppermost bracts, typically a short tube, rarely vestigial and then

reduced to lobed vestiges or, rarely, lacking, the perianth subtended by a ± distinct, erect, tubular perigynium; perianth when mature broadly obconic to ovate, delicate, contracted at the plicate mouth, the mouth 4–6(8)-lobed after extrusion of the capsule, the lobes crenulate by projecting cells. Calyptra with sterile archegonia near its base.

Seta short to moderately long, massive or reduced to 8–10 outer + 3–4 inner rows of cells. Capsule spherical to slightly ovoid, usually 4-valved to the base, the wall 2- or 2–3-stratose; outer layer of cells with strongly nodular thickenings on all but short walls; inner layer of cells with weaker nodular thickenings, often tangentially extended as incomplete or complete semiannular bands (in several taxa with semiannular bands common).

Spores very small, 7–15 μm in diam., the wall obscurely papillate or with low, often furcate, vermiform ridges. Elaters 2- or 3–4-spiral.

Type: *Marsupella emarginata* (Ehrh.) Dumort. (≡ *Jungermannia emarginata* Ehrh.)

A genus of 40–45 species, of which two are bipolar and occur in New Zealand (*Marsupella sprucei*, *M. sparsifolia*). Other Austral species are *M. minutula* Hässel of South Georgia (Hässel, 1980b); *M. capensis* S.W.Arnell of South Africa (Váňa, 1985); *M. lacerata* (Steph.) Váňa of the Neotropics and South Africa (see Váňa, 2003); *M. emarginata* (Ehrh.) Dumort. of wide distribution in the Holarctic and also present in Central Africa (Váňa, 1985; see range in Váňa, 2003); and *M. miniata* (Lindenb. & Gottsche) Grolle (= *M. lorentziana* Steph., type: Argentina, *leg. Lorentz*) occurs in the Neotropics with a range that includes northern Argentina (see Váňa, 2003, p. 122). The genus is absent from Antarctica; the report by Chen et al. (1995) of *M. boeckii* (Austin) Lindb. is actually *Lophozia excisa* (Bednarek-Ochyra et al., 2000). Schuster (2002a) subdivided the genus into five subgenera; the New Zealand species belong to subg. *Marsupella*.

Description adapted and modified from Schuster (2002a).

Key to Species

1a. Leafy shoots minute, to 525 μm wide, 2–5 (rarely 7–8) mm tall; leafy shoots abruptly larger-leaved distally, almost always eventually fertile, the lower leaves often scale-like and ± erect or erect-appressed; spores 13.4–14.9 μm in diam. . . . . *M. sprucei* (p. 799)

1b. Leafy shoots relatively large, to 650–1100 μm wide, 8–15 mm tall; leafy shoots subequally leafy throughout or gradually smaller-leaved below, with strongly and stiffly spreading leaves; spores 9.1–10.6 μm in diam. . . . . *M. sparsifolia* (p. 801)

Subg. ***Marsupella***

Marsupella sprucei (Limpr.) Bernet

[Fig. 177: 9–17]

Sarcoscyphus sprucei Limpr., Jahresber. Schles. Ges. Vaterl. Cult. 179. 1881. *Marsupella sprucei* (Limpr.) Bernet, Cat. Hép. Suisse 33. 1888. *Marsupella ustulata* var. *sprucei* (Limpr.) R.M.Schust., Hepat. Anthocerotae N. Amer. 3: 30. 1974. Type: Germany, Fichtelgebirge, *Funck*.

Plants chocolate-brown to fuscous brown, erect in growth, (270)420–525 μm wide, often repeatedly fertile by frequent innovation from below the ♀ inflorescence, the innovations usually again fertile, the fertile plants often subcapitate in appearance (due to the small lower leaves becoming swiftly larger toward the inflorescence). Branching common in sterile, leafy sectors of shoots, the branches lateral-intercalary, from median, or less often ventral, sector of leaf axil, the plants rather sparingly stoloniferous. Leaves mostly obliquely spreading, only sporadically widely spreading, remote to contiguous below but toward the shoot apices becoming approximate to weakly imbricate, the insertion transverse in dorsal half, the leaf insertions crossing the stem midline dorsally, the leaves adaxially concave, broadly ovate to suboblate, widest a little below the middle, on sterile shoots 300–350 μm wide × 360–410 μm long, often somewhat cordate at the base, bilobed to 0.2–0.3, sometimes a little asymmetrically so, with one lobe slightly larger than the other, lobes acute to subacute, at times feebly apiculate, terminating in a single cell or a uniseriate row of 2 cells (in either case these tip cells as wide as long or wider than long); sinus acute. Cells with bulging trigones, the median lamina cells subisodiametric, 13–17 × 13–18(22) μm, the basal cells 18–20 μm wide × 20–22 μm long; surface ?smooth.

Paroecious. Androecial bracts in 2 pairs, much larger than leaves, erect, suboblate, moderately ventricose in median-basal sector, bifid to ca. 0.25, the lobes rather broadly acute; antheridia 2 per bract, the stalk to 13 cells long, biseriate. Gynoecial bracts erect, mutually involute, sheathing the abbreviated perianth, ± clasping at the base, bilobed to ca. 0.25, the lobes acute to often apiculate. Perianth delicate, low and inconspicuous, formed of variously rectangular cells, those near the mouth hyaline and colorless, the mouth crenulate by cells that are finger-like and free only near the distal end.

Capsule spherical, the wall 2-stratose, outer layer of cells subquadrate to short-rectangular, the radial longitudinal and transverse walls with sharply defined, strong, nodular to weakly spur-like thickenings; inner layer of cells much more irregular, often narrowly rectangular, the longitudinal walls with similar nodular to spur-like thickenings but somewhat smaller, the thickenings rarely extended on the tangential face as complete semiannular bands.

Spores pale brown, 13.4–14.9 μm in diam., the wall with low papillae and short-vermiculate markings; spore:elater diam. ratio 1.4–1.7:1. Elaters slightly tortuous, 8.6–9.6 μm wide, bispiral to tips, the spirals 3.4–4.3 μm wide.

Distribution and Ecology: Bipolar; in New Zealand: South Island (1160–1970 m). In the Southern Hemisphere also known from southern South America (Argentina, Tierra del Fuego, Cerro Garibaldi, 245–275 m). In New Zealand known from Fiordland (Gertrude Valley), Westland (Main Divide near Mt. Brewster; ridge to Mole Tops, Ella Ra.) and Otago (Old Man Ra.) EPs.

In the alpine zone on fully exposed soil among stones, e.g., on track to Gertrude Saddle (head of Gertrude Valley, Fiordland Natl. Park), or on an exposed ridge admixed with *Solenostoma rufiflorum* (below and W of Mt. Armstrong, SSW of Mt. Brewster, Mt. Aspiring Natl. Park). Also on an exposed ridge in penalpine scrub consisting mainly of *Chionochloa*, *Dracophyllum* and *Hebe* (e.g., below and W of Mt. Shrimpton, Mt. Aspiring Natl. Park). On the Old Man Ra. it occurred on damp soil above a snowbank. It has been found with *Bartramia papillata*, *Chrysoblastella chilensis*, *Conostomum pusillum*, *Coprosma petriei*, *Ditrichum brevirostre*, *Grimmia pulvinata*, *Solenostoma totipapillosum* and *Weissia controversa*. Schuster (1996d, p. 66) remarked the ecology of *Marsupella sprucei* "differs from that of *M. sparsifolia*: rather than occurring on soil along rivulets, or on rocks where kept moist by seepage,

M. sprucei s. lat., in the Antipodes, the species occurs on soil, often [at] considerable distances from rock outcrops, and rarely in areas where apt to be submerged," which matches the conditions that we have encountered our two *Marsupella* species in New Zealand. Schuster (1996d, p. 65) also commented that in the Southern Hemisphere, *M. sprucei* occurs in "moist montane, treeless zones—from sites not too dissimilar to those occupied by the species in the Northern Hemisphere."

Comments: The above description is based solely on New Zealand plants. For comments see under *Marsupella sparsifolia*.

Marsupella sparsifolia (Lindb.) Dumort.

Sarcoscyphus sparsifolius Lindb., Not. Pro Fauna Fl. Fenn. 9: 280. 1868. *Marsupella sparsifolia* (Lindb.) Dumort., Hepat. Eur. 128. 1874. *Nardia sparsifolia* (Lindb.) Lindb., Musci Scand. 10. 1879. Type: Scandinavia.

This bipolar species has two subspecies: subspecies *sparsifolia* is "largely Arctic-alpine and high subarctic" and is generally rare and local (Schuster, 1996d, p. 41); subspecies *childii* occurs in our area.

Marsupella sparsifolia subsp. ***childii*** R.M.Schust.

[Figs. 176, 177: 1–8]

Marsupella sparsifolia subsp. *childii* R.M.Schust., J. Hattori Bot. Lab. 80: 61. *f. 10.* 1996. Type: New Zealand, South Is., Fiordland Natl. Park, Mt. Burns track, 4500–5000 ft., *Schuster 84-142*.

Plants erect, fuscous or deep brown, 620–700 μm to 770–1160 μm wide in sterile sectors, 5–9(15) mm high. Branching common in basal sectors of plant, typically absent above, the branches lateral-intercalary, from ventral end of leaf axil; stoloniform axes infrequent or occasional. Stems brownish. Leaves remaining almost identical in size and form to near the gametangial region, almost immediately stiffly laterally spreading and remaining so ± throughout shoot, remote, the bases not at all sheathing, essentially transversely oriented and inserted, the leaves distinctly concave, mostly ± symmetrically ovate to ellipsoidal, rather sharply narrowing toward the base, 360–520 μm wide × 400–620 μm long, bilobed to ca. 0.15–0.2 to 0.3–0.35, sometimes a little asymmetrically so, with one lobe slightly larger than the other; lobes usually sharply acute or subacute, terminating in a single cell or a uniseriate row of 2 cells; sinus usually broadly V-shaped, blunt to subacute at base, sometimes narrowly rounded. Cells with trigones large and convex-sided to knot-like, the cells small, the median cells 12–18 μm wide × 14–22 μm long, the basal cells appreciably larger, 15–22 μm wide × 17–26 μm long; surface smooth or inconspicuously striate. Oil-bodies occupying a conspicuous portion of cell lumen, glistening, appearing whitish, (1)2(4) per median lamina cell, at base more commonly 3 or 4 per cell, granular-finely papillose, at times with a depression, the oil-bodies globose to broad-elliptic, 3.8–4.8 × 6.7–8.6 μm to 5.5–6 × 10–11 μm, spherical ones 4–5.8 μm in diam., if one per cell then often very large.

Paroecious, but fertilized gynoecia infrequent. Androecial bracts abruptly larger than leaves immediately below, in 2–3 pairs, more concave and much larger than leaves, bilobed to ca. 0.2; antheridia 2 per bract, the stalk 10–11 cells long, biseriate. Gynoecial bracts erect,

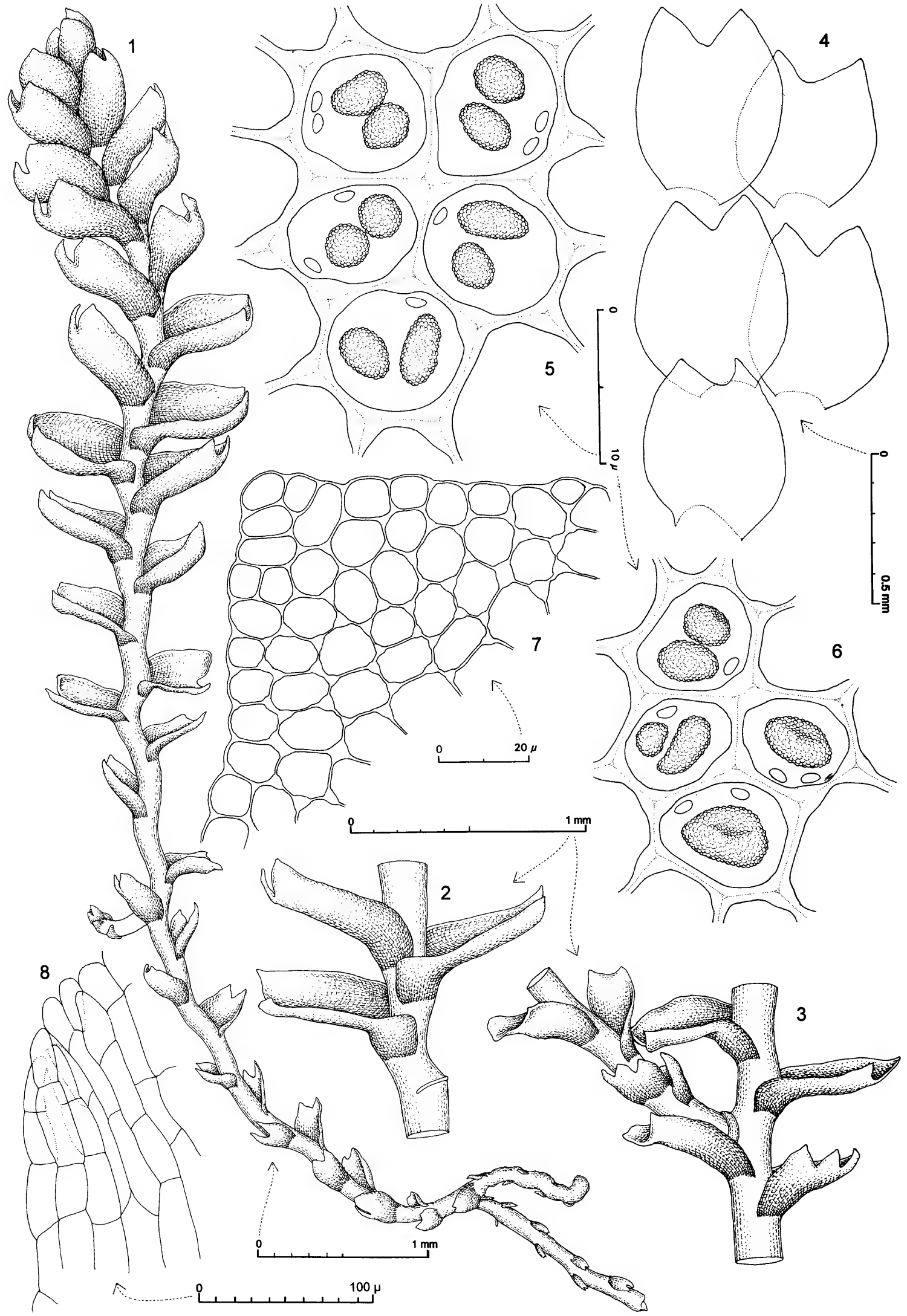

Fig. 176.
Marsupella sparsifolia subsp. *childii* R.M.Schust. 1. Leading shoot with 2 stoloniform, lateral-intercalary branches (dorsal view); note also the stoloniform basal sector of the shoot and the dor-

mutually involute, sheathing the abbreviated perianth, the base ± clasping the stem. Perianth delicate, low, formed of delicate, narrowly rectangular cells, those near the mouth hyaline, colorless and notably leptodermous, the pigmented cells below with distinct trigones; mouth truncate, crenulate by cells that are finger-like and free only near the distal end. Calyptra with sterile archegonia near its base.

Seta with 20 rows of outer cells surrounding an inner core of 23 somewhat smaller cells, the exposed wall rather thick. Capsule spherical, the wall fragile, brittle, 2-stratose, 17–20 μm thick, the outer layer of cells somewhat thicker than inner layer, the outer layer of cells with sharply defined, strong, nodular thickenings that often appear clavate in surface view; inner layer of cells with similar nodular thickenings but moderately to much smaller, semiannular bands rare and isolated.

Spores pale brown, 9.1–10.6 μm in diam., the wall with low but sharply defined, short, often furcate, vermiform ridges; spore:elater diam. ratio 1–1.3:1. Elaters moderately tortuous, 8.2–9.6 μm wide, bispiral to tips, the spirals 2.9–3.8 μm wide.

Distribution and Ecology: New Zealand: Stewart Island (ca. 30 m), South Island (1220–1830 m); subspecies *childii* is endemic to New Zealand. Known from Fiordland (Mt. Burns), Southland (Eyre Mtns.), Otago (head of Wye Creek, Remarkables), Westland (ridge between Young and Blue rivers) and Canterbury (Harman Pass) EPs.

At the margins of rills in the alpine zone (e.g., on the plateau and slopes below Mt. Burns, Fiordland Natl. Park), in seepage areas and on alpine tarn margins, on soil or stones, sometimes in *Oreobolus pectinatus* and *O. pusillus* cushionfield. In these alpine sites it occurs characteristically with *Diplophyllum verrucosum*, but also with *Andreaea acuminata*, *A. subulata*, *Blindia robusta*, *Cephalomitrion aterrimum*, *Cryptochila grandiflora*, *Drepanocladus revolvens*, *Hepatostolonophora rotata* var. *rotata* and *Hygrolembidium acrocladum*. On Stewart Island the plant occurred over bedrock in a very humid niche that is often inundated or totally saturated (at top of Belltopper Falls, Port Pegasus, North Arm). Interestingly, the site is only 30 m elevation. In the upper Wye Creek (Remarkables, Otago, 1830 m) it forms cushions on soil on a tarn margin, which are at times at the water's edge but at other times may be 50 m from the water's edge. On Harman Pass (Main Divide 15 km SW of Arthur's Pass, 1320 m) it occurs on soil at the margins of small tarns among cushionfields of *Oreobolus* and on bedrock kept wet by seepage. Schuster (1996d, p. 64) commented that the taxon "may form extensive mats . . . where subject to submersion, over stones and peaty soil on stones, at the edges of alpine tarns."

Comments: The above description is based solely on New Zealand plants.

This is a larger plant than our other species, *Marsupella sprucei*, being 650–1100 μm wide, 8–15 mm tall vs. to 450 μm wide and typically 2–5 mm tall in *M. sprucei*. Also, the leafy shoots are subequally leafy throughout or only gradually smaller-leaved below in *M. sparsifolia* (Fig. 176: 1) vs. leafy shoots abruptly larger-leaved distally and almost always eventually fertile in *M. sprucei*.

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sally interlocking merophytes. 2. Sector of leading shoot showing leaf insertions crossing stem midline dorsally. 3. Sector of main shoot with a lateral-intercalary branch, dorsal view; note 3-lobed leaf. 4. Five leaves. 5, 6. Median leaf cells with oil-bodies. 7. Portion of leaf lobe. 8. Portion of perianth mouth. (All from *Glenny 9735*, New Zealand, South Is., Canterbury EP, Harman Pass.)

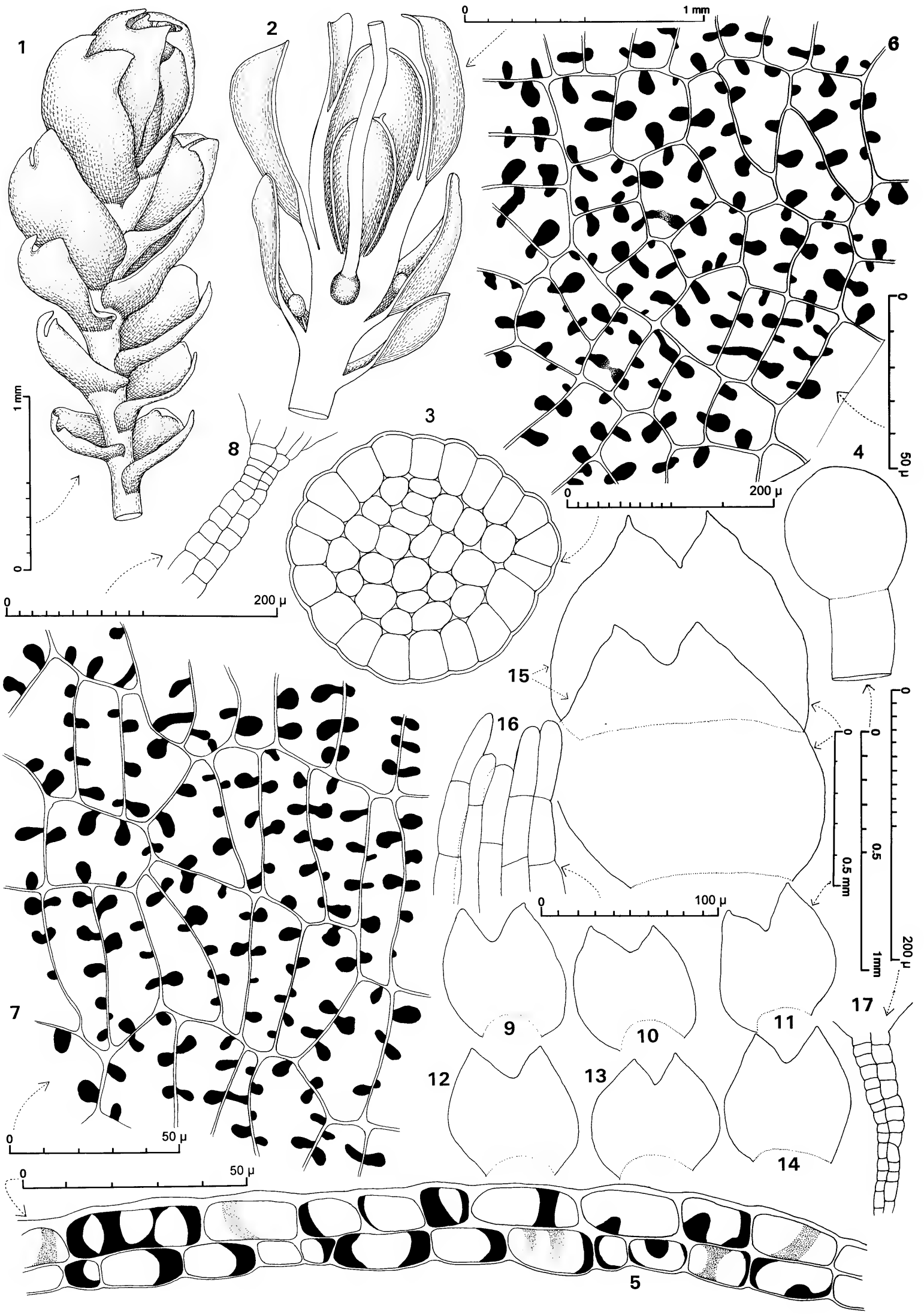

Fig. 177.
Marsupella sparsifolia subsp. *childii* R.M.Schust. (figs. 1–8) and *Marsupella sprucei* (Limpr.) Bernet (figs. 9–17). 1. Mature gynoecium, dorsal view; note capsule dehiscence within the en-

This species may be confused with species of *Allisoniella*, particularly *A. scottii*. The form of the gynoecial apparatus will immediately distinguish *Marsupella* from *Allisoniella*, but problems may occur when only sterile plants are at hand. Two of the three species of *Allisoniella* that occur in New Zealand have sulcate leaf lobes, vs. plane leaf lobes in *M. sparsifolia* (Fig. 176: 1–3); the character may be observed in the field. *Allisoniella scottii*, however, has plane leaf lobes and in such cases one should search for branching modalities: *A. scottii* has ventral-intercalary branches vs. lateral-intercalary in *M. sparsifolia* (Fig. 176: 3). (For further comments see under *Allisoniella scottii*.)

Gymnomitrion Corda

Gymnomitrion Corda *in* Opiz (ed.), Beitr. Naturk. [1]: 651. 1829.
Cesius Gray, Nat. Arr. Brit. Pl. 1: 705. 1821, *nom. rej.* Type: *Cesius concinnatus* (Lightf.) Gray
Acolea Dumort., Syll. Jungerm. Europ. 76. 1831, *nom. illeg.* Type: *Acolea concinnatus* (Lightf.) Dumort.
Cesiusa Kuntze, Revis. Gen. Pl. 833. 1891, *nom. rej.* Type: *Cesiusa concinnata* (Lightf.) Kuntze.
Dianthelia R.M.Schust., Bryologist 52: 103. 1949. Type: *Dianthelia steerei* R.M.Schust.

Plants mostly in dense, compact, pure, typically small cushions, the shoots erect and mutually appressed (less often, and initially in clone formation, procumbent or loosely ascending), julaceous to vermiform, terete to weakly dorsally flattened, distally sometimes ± clavate, silver-whitish or grey, at times grey-green, less frequently yellowish brown or reddish/purplish or piceous to reddish black, rather small, usually 250–750 μm wide. Branching irregular, the branches usually from older shoot sectors, of lateral-intercalary type; *Frullania*-type branches present in a few taxa (e.g., *Gymnomitrion incompletum* of Australia) and then only of isolated occurrence; branches usually of 2 types: erect and leafy and geotropic, microphyllous and stoloniform. Stems slender, relatively soft-textured, a little fleshy, the cortical cells usually weakly thick-walled, not forming a hyaloderm. Rhizoids typically from stolons and older shoot sectors. Leaves erect, densely imbricate, with apex and margins mostly ± appressed to those above, nearly transversely oriented, the insertion broad, virtually transverse (on lax shoot sectors subsuccubous), the leaves concave, broad-based, usually ovate or subrotundate, usually 0.1–0.4(0.55) bifid, rarely unlobed; leaves with apex and margins usually narrowly to extensively decolorate (also lacking oil-bodies); intramarginal lamina cells ± collenchymatous, often with ± bulging trigones, the cells rather small; surface smooth or asperulate. Oil-bodies large, usually 2–3(4) per cell, finely to coarsely granular. Underleaves lacking or comprised of only 2- to few-celled rudiments, sometimes juxtaposed to leaf bases.

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closed ♀ bracts. 2. Longitudinal section through gynoecium with mature sporophyte; note paroecious condition. 3. Seta, cross section. 4. Capsule profile. 5. Capsule wall, cross section. 6. Capsule wall, outer layer. 7. Capsule wall, inner layer. 8. Antheridial stalk. 9–14. Leaves (all drawn to same scale). 15. Bract of innermost series (above) and (below) a bract from series immediately below, both inserted on the perigynium (and note drawn to same scale as leaves). 16. Portion of perianth mouth. 17. Antheridial stalk. (Figs. 1–8, from *Glenny 9735*, New Zealand, South Is., Canterbury EP, Harman Pass; 9–17, from *Engel 17909*, New Zealand, South Is., Otago EP, Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton.)

Dioecious or autoecious. Androecia weakly differentiated from vegetative areas, terminal but soon becoming intercalary; bracts in several pairs, similar to leaves but often slightly larger and more concave or ventricose; antheridia 1–3 per bract, the stalk biseriate. Gynoecia terminal on leading shoots, with several series of closely imbricate, mutually involute, gradually larger, basically leaf-like bracts that typically form a ± clavate "head," within the pair of largest bracts (which may be ± toothed) are 1–several small, often very reduced, multiform, variously incised/lacerate/laciniate innermost bracts (the innermost bracts usually free, sometimes slightly connate). Perianth and perigynium entirely lacking (except *Gymnomitrion apiculatum*, which has a low and distinct perianth and a low subtending perigynium); axial tissue below distal-most bracts ± proliferating as a generalized coelocaule-precursor. Calyptra with unfertilized archegonia usually ± elevated.

Seta short, the capsule barely exserted. Capsule spherical, the wall 2-, 2(3)- or rarely 3-stratose; outer layer of cells with strong, sometimes ± confluent nodular thickenings; inner layer of cells with nodular thickenings, the thickenings smaller than those of the outer layer and distant.

Spores 8–18 μm in diam., distinctly areolate (in ours) or minutely papillose to verruculose. Elaters 6.5–8 μm wide, 2(3–4)-spiral.

Type: *Gymnomitrion concinnatum* (Lightf.) Corda (≡ *Jungermannia concinnata* Lightf.)

A genus of ca. 20 species, with two occurring in our area (*Gymnomitrion cuspidatum*, *G. strictum*). *Gymnomitrion concinnatum* (Lightf.) Corda occurs in Chile (Tierra del Fuego, Fjordo Finlandia, *leg. Roivainen*). Reports of this species from the Southern Hemisphere were shown to be in error by Grolle (1966d) and Schuster (1974a), and the first credible report from the Southern Hemisphere is by Váňa (1976). *Gymnomitrion incompletum* (Gottsche) R.M.Schust. occurs in Tasmania, Victoria and New South Wales (McCarthy, 2003) and *G. laceratum* (Steph.) Horik. is present in South and Central Africa. The genus is absent from Antarctica; the report by Chen et al. (1995) of *G. corallioides* Nees is actually *Herzogobryum teres* (Bednarek-Ochyra et al., 2000).

Both of our species are autoecious, unlike the majority members of the genus.

Treatment of genus adapted and modified from Schuster (1996d).

References: Berggren (1898); Grolle (1966d); Schuster (1996d, 2002a).

Key to Species

1a. Leaves (0.25)0.3–0.45(0.5) bilobed; leaf lobes distinctly asperulate; plants whitish green (the leaf apices and margins decolorate); leafy shoots a little dorsiventrally compressed, the leaves erect to obliquely spreading. Leaf lobes terminating in 1–3 cells . . . . . *G. cuspidatum* (p. 807)

1b. Leaves 0.15–0.25 bilobed; leaf lobes faintly to moderately asperulate; plants yellowish brown pigmented (the leaf apices and margins decolorate); leafy shoots subterete, with dense, erect-appressed leaves. Leaf lobes terminating in a single cell . . . . . *G. strictum* (p. 809)

Gymnomitrion cuspidatum (Berggr.) R.M.Schust.

[Plate 16E]

Cesia cuspidata Berggr., On New Zealand Hepat. 1. *f. 1*. 1898. *Acolea cuspidata* (Berggr.) Steph., Sp. Hepat. 2: 7. 1901. *Gymnomitrion cuspidatum* (Berggr.) R.M.Schust., J. Hattori Bot. Lab. 26: 280. 1963. Type: New Zealand, South Is., Porter's Pass, Mt. Torlesse, 1200 m, Feb. 1874, *Berggren*; South Is., Bealey River, Otira Gorge, Feb. 1874, *Berggren*.

Plants rather fleshy, soft-textured when moist, prostrate but with shoot apices ± ascending, whitish green to whitish, appearing bleached, the shoots densely leafy, somewhat complanate, flattened dorsally, strongly convex ventrally (due to the markedly dorsally assurgent, closely imbricate leaves), the shoots to 1.3 mm wide. Branching sparing to common, the branches all lateral-intercalary; microphyllous geotropic axes rare to sparingly developed. Leaves largely hyaline, vertically oriented, notably dorsally assurgent, mostly obliquely laterally spreading, ranging to suberect, densely imbricate, the stem hidden or virtually so, loosely complanate, the dorsal margins of the leaves erect to narrowly reflexed, the dorsal bases extended across the stem, collectively defining an obscure to distinct longitudinal groove on the dorsal face of the shoot; leaves ovate to elliptic-ovate to elliptic-rectangular, often a little asymmetrical, with one side somewhat more arched than the other, 220–315 μm wide × 399–480 μm long to 450–485 μm wide × 650–715 μm long, bifid to (0.25)0.3–0.45(0.5), the sinus acute; lobes ± parallel, or, more often, feebly divergent (then distal half of leaf almost parallel-sided), their tips usually somewhat divergent, the lobes acute, sharp, cuspidate, long drawn out, terminating in 1–2 elongated (or 2–3 shorter) cells, the lobe margins plane and not recurved, entire or only weakly crenulate by projecting walls of the marginal row of cells. Cells maximally incrassate, the walls very thick, hyaline (hence the whitish color, becoming bleached in appearance when dry), the middle lamella perceptible; cells everywhere guttulate, in lobe apices very strongly thick-walled both on their surfaces (hence cell outlines often rather obscure) and between cells, the lumina mostly ellipsoidal to lozenge-shaped, sometimes linear on lobe margins, quite variable in size and shape; cells in lobe apices and margins often narrow and oriented parallel to margin or obliquely to margin, small, 12–17 × 13–20 μm, the lumina reduced; cells of lobes within margins mostly longitudinally oriented and with ellipsoidal lumina; cells of median portion of lamina somewhat less thick-walled than in lobes, 14–19 × 19–30 μm to 15–18 × (26)30–36(40) μm; surface often distinctly asperulate (at times barely perceptibly so). Underleaves lacking.

Autoecious. Androecia terminal but becoming intercalary on long axes; bracts leaf-like, but with bases shallowly ventricose and lobe margins sporadically crenulate-denticulate; antheridia 1 per bract (always?). Gynoecia usually on lateral-intercalary branches of variable length, sometimes quite abbreviated and not developing mature leaves prior to bract development; bracts grading gradually into leaves, closely imbricate, typically two-ranked in such a manner as to leave a perceptible dorsal groove; innermost bracts narrowly oblong, bifid to 0.4–0.45, the lobes narrowly acute, sporadically with 1–few sharp, 1(2)-celled teeth, the flanks often with a coarse tooth below the lobe bases; within the pair of largest bracts are 2(3) multiform, somewhat abbreviated, pleated and variably 3–4(5)-lobed structures (?derived by reduction from the perianth), the lobes irregular, tapered, acuminate to caudate, mostly bearing a few sharp, remote, 1–2-celled, often arched, spinose teeth; innermost reduced bractlets (always?) absent. Perianth wholly lacking.

Seta short, elevating capsule not far beyond level of bracts. Capsule spherical, the wall 2-stratose, the wall 18–19 μm thick, the outer layer of cells 3× the thickness of inner layer, the outer layer of cells with two-phase development, the longitudinal walls bearing low, rounded, occasionally ± coalescent nodular thickenings lending a distinctly sinuous appearance alternating with walls devoid of thickenings or with isolated smaller nodular thickenings, the transverse walls lacking thickenings or sporadically with a solitary low thickening; inner layer of cells with longitudinal walls bearing well-developed, low, rounded, often coalescent nodular thickenings lending a distinctly sinuous appearance, the pattern rather similar to the outer wall but the thickenings not as strongly developed, the transverse walls often with nodular thickenings but these smaller than those of the vertical walls.

Spores red-brown, 13.9–14.9 μm in diam. distinctly areolate, the ridges rather thick. Elaters not seen.

Distribution and Ecology: Endemic to New Zealand: South Island ([520]1000–1480 m), North Island (1350–1660 m). Known from Fiordland (Mt. Burns, Lake Monk), Westland, Otago (Rock and Pillar Ra.), Canterbury, Western Nelson (Lookout Ra.) and Volcanic Plateau EPs.

Rather common in the penalpine and alpine zones over rock or in pockets between boulders or outcrops, particularly where soil has accumulated. Also on flat rock of cliff faces. The species is able to tolerate considerable exposure, e.g., occurring over bare soil of an exposed ridge at 1250–1450 m in alpine vegetation (below and W of Mt. Armstrong, Mt. Aspiring Natl. Park). It exceptionally occurs in forests, e.g., over a shaded cliff face in a *Nothofagus menziesii* forest at 760–800 m (Governors Bush, Mt. Cook Natl. Park) and on the roof of a rock overhang in a *N. menziesii* forest at Haast Pass (540 m) with *Lepidozia pumila*. Plants often occur as isolated stems or they may be gregarious and form thin mats. It is associated with *Andreaea mutabilis*, *Arthroraphis alpina*, *Bartramia papillata*, *Cryptochila grandiflora*, *Dicranoweisia antarctica*, *Diplophyllum domesticum*, *Ditrichum brevirostre*, *Grimmia incrassicapsulis* and *Racomitrium crispulum*.

Comments: This species and *Gymnomitrion strictum* are quite variable and need to be carefully compared utilizing large suites of specimens. Sinus depth, the degree of surface roughening (both species are variously asperulate) and pigmentation all are to some degree variable. In general, however, plants of *G. cuspidatum* are whitish green, with pigmentation only sparsely developed, have leaves more deeply lobed with leaf lobes distinctly asperulate. Plants of *G. strictum*, on the other hand, are nearly always pigmented, have leaves more shallowly lobed, with leaf lobes weakly and often indistinctly asperulate. Schuster (2002a, p. 569) remarks that plants of *G. cuspidatum* are "virtually devoid of brownish pigments; in the field there is a distinct whitish green or whitish aspect to the plants."

Sinus depth should be measured with care, since leaves, when flattened, often tear at the sinus base. Prior to measurements the sinus should be examined under higher magnification to determine the extent of the tear; uneven cell walls often will indicate tear presence and the asperulate surface will indicate absence.

The two New Zealand species are unique in the genus in having distinctly areolate spores.

Gymnomitrion strictum (Berggr.) R.M.Schust.

[Fig. 175: 4, oil-bodies, p. 787]

Cesia stricta Berggr., On New Zealand Hepat. 2. *f. 2*. 1898. *Acolea stricta* (Berggr.) Steph., Sp. Hepat. 2: 7. 1901. *Gymnomitrion strictum* (Berggr.) R.M.Schust., J. Hattori Bot. Lab. 26: 280. 1963. Type: New Zealand, North Is., Mt. Ruapehu, 1500 m, Jan. 1875, *Berggren*.

Plants laxly caespitose to procumbent, locally pale yellowish brown to fulvous brown (the leaf lobes and disc margins decolorate), weakly nitid when dry, the shoots very densely leaved, subterete to somewhat dorsiventrally flattened (then strongly convex ventrally, almost flat dorsally), to 475 μm wide. Branching sparing to irregular (var. *strictum*) to copious and often clustered (var. *inaequalis*), always lateral-intercalary; geotropic stolons usually few or rare. Stems almost colorless, pellucid, the cortex poorly differentiated, the cortical and medullary cells similar in diameter, both somewhat firm-walled, the exposed walls of the cortical cells at times thicker, at times bulging. Rhizoids few or rare, tending to be in small groups from near ventral leaf bases. Leaves erect-appressed, at times slightly dorsally assurgent, markedly densely imbricate, the stem nowhere visible, the median and basal sectors strongly concave, the hyaline margins and lobes nearly flat and appressed to anterior leaf; leaves narrowly to rather broadly ovate and 320–400 μm wide × 350–560 μm long to 400–420 μm wide × 600–625 μm long, bilobed to 0.15–0.25; lobes ± parallel, acute, often apiculate, terminating in a single, isodiametric to often slightly elongated cell, the lobe margins plane and not recurved, entire or crenulate by bulging walls of marginal row of cells; sinus acute to rectangulate, V-shaped, at times the sides flaring. Cells in lobe tips and margins thick-walled, lumina usually guttulate, the cells small, 10–17 μm wide × 11–20 μm long, mostly somewhat elongated parallel to margins in the lobes, less elongated on margins below the lobes; cells within lobes remaining guttulate (var. *inaequalis*) or developing coarse, if ill-defined, trigones, the cells in lamina middle 11–20 × 17–26 μm, those near the base distinctly larger and 15–21 μm wide × (20)25–35(40) μm long; surface faintly to moderately asperulate. Oil-bodies occupying small volume of cell, hyaline, 2–4(5) per cell, coarsely granular, irregularly elliptic to irregularly linear, less often subglobose, 2.4–3.4 × 5.8–7.2 μm to 4.3 × 5.3 μm, a few long-linear and 2.4 × 7.7 μm, subspherical ones 3.4 μm in diam. Chloroplasts exceptionally large for cell size. Underleaves lacking.

Autoecious. Androecia a little broader than sterile leafy sectors, usually (always?) on lateral-intercalary branches, at times arising almost juxtaposed to the ♀ branches; bracts in many pairs (8–16 or more), densely imbricate, leaf-like, the lobes sometimes a little more crenulate with projecting cells, the base moderately ventricose; antheridia 1–2 per bract, the stalk 2-seriate. Gynoecia (always?) on lateral-intercalary branches, initially microphyllous and slender, usually soon leafy and, after 8–20 gyres, gynoecial, the gynoecium swollen and clavate, with bracts progressively much larger, erect-appressed, but dorsal margins often a little reflexed; innermost bracts large, free dorsally, otherwise connate to 0.5 or more into a strongly plicate sheath with ca. 5–6 major lobes (2–3 per bract, 1 representing the bracteole?, the intervening sinuses descending to 0.3), each lobe long-acute (var. *strictum*) ranging to long-acuminate or piliferous (var. *inaequalis*) and with margins crenulate to dentate; accessory, reduced bractlets often present within the connate innermost bracts, small, variable, sometimes lanceolate, 0.35–0.45 the length of the bracts. Perianth completely lacking. Calyptra with sterile archegonia at base.

Seta seen only in collapsed state. Capsule wall 2-stratose, 22–26 μm thick, the outer layer of cells with one-phase development, the longitudinal walls typically bearing very strong, ± coalescent, nodular thickenings lending a sinuous appearance, the transverse walls lacking thickenings or sporadically with a solitary thickening; inner layer of cells mostly less regular, with weak or small, widely separated nodular thickenings on all but the shortest walls, the thickenings moderately to distinctly smaller than those of the outer wall.

Spores pale reddish brown, 16.3–18.2 μm in diam., distinctly areolate, the ridges rather thick. Elaters not seen.

Distribution and Ecology: Endemic to New Zealand: Campbell Island (450 m), South Island (1040–2130 m), North Island (1200–1700 m). Known from Fiordland, Westland, Otago, Canterbury, Marlborough (Seaward and Inland Kaikoura ranges) and Volcanic Plateau EPs.

Occurring in the penalpine and alpine zones in rock crevices, on boulder faces, as well as in niches between boulders or, in Central Otago, on the schist tors. At times in shaded, more protected sites such as on the undersides of dripping ledges or deep under protective overhangs. In the penalpine zone occurring, for example, on a boulder face in an exposed stream valley through scrub of *Halocarpus bidwillii*, *Ozothamnus leptophyllus* and *Phyllocladus alpinus* (Taranaki Falls track, Tongariro Natl. Park, 1240 m). It has been found with *Andreaea acutifolia*, *A. mutabilis*, *Andrewsianthus cuspidatus*, *Bartramia papillata*, *Conostomum pentastichum*, *Cryptochila grandiflora*, *Diplophyllum domesticum*, *Ditrichum punctulatum*, *Herbertus oldfieldianus*, *Herzogobryum teres*, *Hymenophyllum armstrongii*, *Notholigotrichum australe*, *Nothogymnomitrion erosum*, *Rhacocarpus purpurascens* and *Siphula rubra*.

Comments: Plants of this species occasionally are completely bleached and then have the appearance of *Anthelia*, a plant with rather similar leaf shape and areolation. The absence of underleaves and the larger plant size will immediately distinguish such plants as *Gymnomitrion*. For other comments see under *G. cuspidatum*.

Two varieties have been recognized as follows; these require evaluation based upon the study of more material.

Key to Varieties

1a. Shoots sparingly and irregularly branched; leaf lobes equal or almost so, their apices never divergent; cells guttulate only in leaf tips and upper margins, becoming collenchymatous in lobe bases and middle; ♀ bracts with lobes acute, never long-acuminate . . . . . var. *strictum* (p. 810)

1b. Shoots copiously branched; leaf lobes unequal, their tips often divergent; cells guttulate throughout the lobes and into the leaf middle; ♀ bracts with lobes often acuminate to piliferous, sometimes terminating in a uniseriate row of 5–7 cells . . . . . var. *inaequalis* (p. 811)

Gymnomitrion strictum (Berggr.) R.M.Schust. var. ***strictum***

Plants with branching sparse, irregular. Leaves ovate, the lobes symmetrically developed, erect, the tips never conspicuously divergent, terminating in a single cell that is usually little

elongated. Cells in lobe tips and in the hyaline margins thick-walled to guttulate, within the lobes becoming somewhat elongated, developing ill-defined but sometimes perceptible trigones; cells of lobe bases and leaf middle more often little elongated or subisodiametric, remaining firm-walled but developing coarse and often nodose or nodose-confluent trigones.

♀ Bracts with lobes acute but never long-acuminate.

Gymnomitrion strictum var. ***inaequalis*** R.M.Schust.

Gymnomitrion strictum var. *inaequalis* R.M.Schust., J. Hattori Bot. Lab. 80: 118. *f. 21: 1–4, 22.* 1996. Holotype: New Zealand, South Is., Fiordland Natl. Park, track from Lake Mackenzie to Harris Saddle, Humboldt Mtns., 3800–4000 ft., *Schuster 67-386b*.

Plants with branching copious, the longer sterile axes sometimes laxly pinnulate, with wide-spreading arcuate branches that may remain ± abbreviated. Leaves with lobe apices often somewhat divergent, the lobes usually terminating in a single but often ± elongated cell. Cells of lobe margins quite thick-walled, the lumina guttulate, subquadrate to short-oblong; intramarginal lobe cells remaining guttulate, the lumina mostly elliptical, becoming appreciably but gradually larger from margins; cells from middle to base of leaf becoming considerably larger, less firm-walled, more angular.

Gynoecia with lobes of innermost bracts erect, narrow, lanceolate-acuminate, often setigerous distally and terminating in a uniseriate row of 5–7 cells, the bract margins crenulate-denticulate to denticulate and, below, sometimes with 1–2 teeth.

APPENDIX
SPECIES MENTIONED IN THIS VOLUME

Monocots

Agrostis capillaris L.	*Poaceae*
Anthoxanthum odoratum L.	*Poaceae*
Astelia linearis Hook.f.	*Liliaceae*
Astelia subulata (Hook.f.) Cheeseman	*Liliaceae*
Astelia trinervia Kirk	*Liliaceae*
Baumea tenax (Hook.f.) S.T.Blake	*Cyperaceae*
Baumea teretifolia (R.Br.) Palla	*Cyperaceae*
Bulbinella hookeri (Hook.) Cheeseman	*Liliaceae*
Bulbinella rossii (Hook.f.) Cheeseman	*Liliaceae*
Carex gaudichaudiana Kunth	*Cyperaceae*
Carex secta Boott	*Cyperaceae*
Carex sinclairii Boott	*Cyperaceae*
Carpha alpina R.Br.	*Cyperaceae*
Centrolepis ciliata (Hook.f.) Druce	*Centrolepidaceae*
Chionochloa antarctica (Hook.f.) Zotov	*Poaceae*
Chionochloa australis (Buchanan) Zotov	*Poaceae*
Chionochloa conspicua (G.Forst.) Zotov	*Poaceae*
Chionochloa crassiuscula (Kirk) Zotov	*Poaceae*
Chionochloa flavescens Zotov	*Poaceae*
Chionochloa juncea Zotov	*Poaceae*
Chionochloa lanea Connor	*Poaceae*
Chionochloa macra Zotov	*Poaceae*
Chionochloa oreophila (Petrie) Zotov	*Poaceae*
Chionochloa pallens Zotov	*Poaceae*
Chionochloa pungens (Cheeseman) Zotov	*Poaceae*
Chionochloa rigida (Raoul) Zotov	*Poaceae*
Chionochloa rubra Zotov	*Poaceae*
Empodisma minus (Hook.f.) L.A.S.Johnson & D.F.Cutler	*Restionaceae*
Festuca matthewsii (Hack.) Cheeseman	*Poaceae*
Freycinetia baueriana Endl.	*Pandanaceae*
Gahnia procera J.R.Forst. & G.Forst.	*Cyperaceae*
Gahnia xanthocarpa (Hook.f.) Hook.f.	*Cyperaceae*
Luzula colensoi Hook.f.	*Juncaceae*
Luzuriaga parviflora (Hook.f.) Kunth	*Smilacaceae*
Marsippospermum gracile (Hook.f.) Buchenau	*Juncaceae*
Microlaena avenacea (Raoul) Hook.f.	*Poaceae*
Oreobolus impar Edgar	*Cyperaceae*
Oreobolus pectinatus Hook.f.	*Cyperaceae*
Phormium cookianum Le Jol.	*Agavaceae*
Phormium tenax J.R.Forst. & G.Forst.	*Agavaceae*
Poa cita Edgar	*Poaceae*

Poa colensoi Hook.f.	*Poaceae*
Rhopalostylis sapida H.Wendl. & Drude	*Arecaceae*
Ripogonum scandens J.R.Forst. & G.Forst.	*Smilacaceae*
Rostkovia magellanica (Lam.) Hook.f.	*Juncaceae*
Rytidosperma setifolium (Hook.f.) Connor & Edgar	*Poaceae*
Schoenus pauciflorus (Hook.f.) Hook.f.	*Cyperaceae*
Sporadanthus ferrugineus de Lange, Heenan & B.D.Clarkson	*Restionaceae*
Typha orientalis C.Presl	*Typhaceae*
Zotovia colensoi (Hook.f.) Edgar & Connor	*Poaceae*

Dicots

Ackama rosifolia A.Cunn.	*Cunoniaceae*
Alectryon excelsus Gaertn.	*Sapindaceae*
Anisotome aromatica Hook.f.	*Apiaceae*
Anisotome latifolia Hook.f.	*Apiaceae*
Archeria traversii Hook.f.	*Epacridaceae*
Aristotelia serrata (J.R.Forst. & G.Forst.) W.R.B.Oliv.	*Elaeocarpaceae*
Ascarina lucida Hook.f.	*Chloranthaceae*
Beilschmiedia tarairi (A.Cunn.) Benth. & Hook.f. *ex* Kirk	*Lauraceae*
Beilschmiedia tawa (A.Cunn.) Benth. & Hook.f. *ex* Kirk	*Lauraceae*
Brachyglottis buchananii (J.B.Armstr.) B.Nord.	*Asteraceae*
Brachyglottis rotundifolia J.R.Forst. & G.Forst.	*Asteraceae*
Callitriche L.	*Callitrichaceae*
Calluna vulgaris (L.) Hull	*Ericaceae*
Carpodetus serratus J.R.Forst. & G.Forst.	*Grossulariaceae*
Celmisia angustifolia Cockayne	*Asteraceae*
Celmisia armstrongii Petrie	*Asteraceae*
Celmisia discolor Hook.f.	*Asteraceae*
Celmisia monroi Hook.f.	*Asteraceae*
Celmisia petiolata Hook.f.	*Asteraceae*
Celmisia spectabilis Hook.f.	*Asteraceae*
Chionohebe pulvinaris (Hook.f.) B.G.Briggs & Ehrend.	*Scrophulariaceae*
Coprosma chathamica Cockayne	*Rubiaceae*
Coprosma foetidissima J.R.Forst. & G.Forst.	*Rubiaceae*
Coprosma grandifolia Hook.f.	*Rubiaceae*
Coprosma petriei Cheeseman	*Rubiaceae*
Coprosma pseudocuneata W.R.B.Oliv. *ex* Garn.-Jones & Elder	*Rubiaceae*
Coprosma rhamnoides A.Cunn.	*Rubiaceae*
Coprosma rigida Cheeseman	*Rubiaceae*
Coprosma robusta Raoul	*Rubiaceae*
Coprosma rotundifolia A.Cunn.	*Rubiaceae*
Coprosma tayloriae A.P.Druce *ex* G.T.Jane	*Rubiaceae*
Coriaria L.	*Coriariaceae*
Corokia buddleioides A.Cunn.	*Cornaceae*
Corokia macrocarpa Kirk	*Cornaceae*

APPENDIX

Corynocarpus laevigatus J.R.Forst. & G.Forst.	*Corynocarpaceae*
Cyathodes empetrifolia (Hook.f.) Hook.f.	*Epacridaceae*
Cyathodes fasciculata (G.Forst.) Allan	*Epacridaceae*
Dracophyllum arboreum Cockayne	*Epacridaceae*
Dracophyllum longifolium (J.R.Forst. & G.Forst.) R.Br.	*Epacridaceae*
Dracophyllum politum (Cheeseman) Cockayne	*Epacridaceae*
Dracophyllum pronum W.R.B.Oliv.	*Epacridaceae*
Dracophyllum recurvum Hook.f.	*Epacridaceae*
Dracophyllum rosmarinifolium (G.Forst.) R.Br.	*Epacridaceae*
Dracophyllum scoparium Hook.f.	*Epacridaceae*
Dracophyllum subulatum Hook.f.	*Epacridaceae*
Dracophyllum traversii Hook.f.	*Epacridaceae*
Drosera arcturi Hook.	*Droseraceae*
Drosera spathulata Labill.	*Droseraceae*
Dysoxylum spectabile (G.Forst.) Hook.f.	*Meliaceae*
Elaeocarpus dentatus (J.R.Forst. & G.Forst.) Vahl	*Elaeocarpaceae*
Elaeocarpus hookerianus Raoul	*Elaeocarpaceae*
Eucalyptus obliqua L'Hér.	*Myrtaceae*
Euchiton mackayi (Buchanan) Anderb.	*Asteraceae*
Forstera mackayi Allan	*Stylidiaceae*
Forstera sedifolia G.Forst.	*Stylidiaceae*
Forstera tenella Hook.f.	*Stylidiaceae*
Fuchsia excorticata (J.R.Forst. & G.Forst.) L.f.	*Onagraceae*
Gaultheria depressa Hook.f.	*Ericaceae*
Gentianella divisa (Kirk) Glenny	*Gentianaceae*
Griselinia littoralis Raoul	*Cornaceae*
Hebe odora (Hook.f.) Cockayne	*Scrophulariaceae*
Hebe subalpina (Cockayne) Andersen	*Scrophulariaceae*
Hectorella caespitosa Hook.f.	*Portulacaceae*
Hoheria angustifolia Raoul	*Malvaceae*
Ixerba brexioides A.Cunn.	*Grossulariaceae*
Knightia excelsa R.Br.	*Proteaceae*
Kunzea ericoides (A.Rich.) Joy Thomps.	*Myrtaceae*
Leptinella dioica Hook.f.	*Asteraceae*
Leptinella maniototo (Petrie) D.G.Lloyd & C.J.Webb	*Asteraceae*
Leptospermum scoparium J.R.Forst. & G.Forst.	*Myrtaceae*
Leucogenes grandiceps (Hook.f.) Beauverd	*Asteraceae*
Litsea calicaris (A.Cunn.) Benth. & Hook.f. *ex* Kirk	*Lauraceae*
Melicytus chathamicus (F.Muell.) Garn.-Jones	*Violaceae*
Melicytus ramiflorus J.R.Forst. & G.Forst.	*Violaceae*
Metrosideros diffusa (G.Forst.) Sm.	*Myrtaceae*
Metrosideros excelsa Sol. *ex* Gaertn.	*Myrtaceae*
Metrosideros kermadecensis W.R.B.Oliv.	*Myrtaceae*
Metrosideros parkinsonii Buchanan	*Myrtaceae*
Metrosideros robusta A.Cunn.	*Myrtaceae*
Metrosideros umbellata Cav.	*Myrtaceae*
Myrsine chathamica F.Muell.	*Myrsinaceae*

Myrsine divaricata A.Cunn.	*Myrsinaceae*
Nertera balfouriana Cockayne	*Rubiaceae*
Nertera villosa B.H.Macmill. & R.Mason	*Rubiaceae*
Nothofagus fusca (Hook.f.) Oerst.	*Nothofagaceae*
Nothofagus menziesii (Hook.f.) Oerst.	*Nothofagaceae*
Nothofagus truncata (Colenso) Cockayne	*Nothofagaceae*
Olearia colensoi Hook.f.	*Asteraceae*
Olearia ilicifolia Hook.f.	*Asteraceae*
Olearia lacunosa Hook.f.	*Asteraceae*
Olearia lyallii Hook.f.	*Asteraceae*
Olearia rani (A.Cunn.) Druce	*Asteraceae*
Ourisia lactea (L.B.Moore) Arroyo	*Scrophulariaceae*
Ozothamnus leptophyllus (G.Forst.) Breitw. & J.M.Ward	*Asteraceae*
Phyllachne colensoi (Hook.f.) Berggr.	*Stylidiaceae*
Pittosporum eugenioides A.Cunn.	*Pittosporaceae*
Pleurophyllum hookeri Buchanan	*Asteraceae*
Pleurophyllum speciosum Hook.f.	*Asteraceae*
Pseudopanax colensoi (Hook.f.) Philipson	*Araliaceae*
Pseudowintera colorata (Raoul) Dandy	*Winteraceae*
Psychrophila obtusa (Cheeseman) W.A.Weber	*Ranunculaceae*
Quintinia serrata A.Cunn.	*Grossulariaceae*
Ranunculus insignis Hook.f.	*Ranunculaceae*
Raoulia grandiflora Hook.f.	*Asteraceae*
Raukawa simplex (G.Forst.) A.D.Mitch., Frodin & Heads	*Araliaceae*
Schefflera digitata J.R.Forst. & G.Forst.	*Araliaceae*
Syzygium maire (A.Cunn.) Sykes & Garn.-Jones	*Myrtaceae*
Ulex europaeus L.	*Fabaceae*
Vitex lucens Kirk	*Verbenaceae*
Weinmannia racemosa L.f.	*Cunoniaceae*
Weinmannia silvicola Sol. *ex* A.Cunn.	*Cunoniaceae*

Conifers

Agathis australis (D.Don) Lindl.	*Araucariaceae*
Dacrycarpus dacrydioides (A.Rich.) de Laub.	*Podocarpaceae*
Dacrydium cupressinum Lamb.	*Podocarpaceae*
Halocarpus bidwillii (Kirk) Quinn	*Podocarpaceae*
Halocarpus biformis (Hook.) Quinn	*Podocarpaceae*
Lagarostrobos colensoi (Hook.) Quinn	*Podocarpaceae*
Lepidothamnus intermedius (Kirk) Quinn	*Podocarpaceae*
Lepidothamnus laxifolius (Hook.f.) Quinn	*Podocarpaceae*
Libocedrus bidwillii Hook.f.	*Cupressaceae*
Libocedrus plumosa (D.Don) Sarg.	*Cupressaceae*
Phyllocladus alpinus Hook.f.	*Phyllocladaceae*
Phyllocladus glaucus Carrière	*Phyllocladaceae*
Phyllocladus trichomanoides D.Don	*Phyllocladaceae*

Pinus radiata D.Don	*Pinaceae*
Podocarpus hallii Kirk	*Podocarpaceae*
Podocarpus nivalis Hook.	*Podocarpaceae*
Podocarpus totara G.Benn. *ex* D.Don	*Podocarpaceae*
Prumnopitys ferruginea (D.Don) de Laub.	*Podocarpaceae*
Prumnopitys taxifolia (D.Don) de Laub.	*Podocarpaceae*

Ferns

Adiantum L.	*Pteridaceae*
Asplenium bulbiferum G.Forst.	*Aspleniaceae*
Azolla Lam.	*Salviniaceae*
Blechnum chambersii Tindale	*Blechnaceae*
Blechnum colensoi (Hook.f. in Hook.) N.A.Wakef.	*Blechnaceae*
Blechnum discolor (G.Forst.) Keys	*Blechnaceae*
Blechnum filiforme (A.Cunn.) Ettingsh.	*Blechnaceae*
Blechnum minus (R.Br.) Ettingsh.	*Blechnaceae*
Blechnum nigrum (Colenso) Mett.	*Blechnaceae*
Blechnum novae-zelandiae T.C.Chambers & P.A.Farrant	*Blechnaceae*
Blechnum procerum (G.Forst.) Sw.	*Blechnaceae*
Cyathea dealbata (G.Forst.) Sw.	*Cyatheaceae*
Cyathea medullaris (G.Forst.) Sw.	*Cyatheaceae*
Cyathea smithii Hook.f.	*Cyatheaceae*
Dicksonia fibrosa Colenso	*Dicksoniaceae*
Dicksonia squarrosa (G.Forst.) Sw.	*Dicksoniaceae*
Gleichenia dicarpa R.Br.	*Gleicheniaceae*
Gleichenia microphylla R.Br.	*Gleicheniaceae*
Grammitis billardierei Willd.	*Grammitidaceae*
Grammitis poeppigiana (Mett.) Pic.Serm.	*Grammitidaceae*
Hymenophyllum armstrongii (Baker) Kirk	*Hymenophyllaceae*
Hymenophyllum bivalve (G.Forst.) Sw.	*Hymenophyllaceae*
Hymenophyllum demissum (G.Forst.) Sw.	*Hymenophyllaceae*
Hymenophyllum ferrugineum Colla	*Hymenophyllaceae*
Hymenophyllum flabellatum Labill.	*Hymenophyllaceae*
Hymenophyllum malingii (Hook.) Mett.	*Hymenophyllaceae*
Hymenophyllum minimum A.Rich.	*Hymenophyllaceae*
Hymenophyllum multifidum (G.Forst.) Sw.	*Hymenophyllaceae*
Hymenophyllum revolutum Colenso	*Hymenophyllaceae*
Hymenophyllum sanguinolentum (G.Forst.) Sw.	*Hymenophyllaceae*
Leptopteris superba (Colenso) C.Presl	*Osmundaceae*
Polystichum vestitum (G.Forst.) C.Presl	*Dryopteridaceae*
Pteridium esculentum (G.Forst.) Cockayne	*Dennstaedtiaceae*
Pyrrosia eleagnifolia (Bory) Hovenkamp	*Polypodiaceae*
Schizaea Sm.	*Schizaeaceae*
Trichomanes elongatum A.Cunn.	*Hymenophyllaceae*
Trichomanes venosum R.Br.	*Hymenophyllaceae*

APPENDIX

Mosses

Achrophyllum dentatum (Hook.f. & Wilson) Vitt & Crosby	*Hookeriaceae*
Achrophyllum quadrifarium (Sm.) Vitt & Crosby	*Hookeriaceae*
Andreaea acuminata Mitt.	*Andreaeaceae*
Andreaea acutifolia Hook.f. & Wilson	*Andreaeaceae*
Andreaea mutabilis Hook.f. & Wilson	*Andreaeaceae*
Andreaea nitida Hook.f. & Wilson	*Andreaeaceae*
Andreaea subulata Harv.	*Andreaeaceae*
Bartramia papillata Hook.f. & Wilson	*Bartramiaceae*
Blindia immersa (E.B.Bartram & Dixon) Sainsbury	*Seligeriaceae*
Blindia magellanica Schimp.	*Seligeriaceae*
Blindia robusta Hampe	*Seligeriaceae*
Brachythecium paradoxum (Hook.f. & Wilson) A.Jaeger	*Brachytheciaceae*
Brachythecium rutabulum (Hedw.) Bruch & Schimp.	*Brachytheciaceae*
Braithwaitea sulcata (Hook.) A.Jaeger	*Hypnodendraceae*
Breutelia elongata (Hook.f. & Wilson) Mitt.	*Bartramiaceae*
Breutelia pendula (Sm.) Mitt.	*Bartramiaceae*
Bryum blandum Hook.f. & Wilson	*Bryaceae*
Bryum laevigatum Hook.f. & Wilson	*Bryaceae*
Calliergonella cuspidatum (Hedw.) Loeske	*Amblystegiaceae*
Calomnion complanatum (Hook.f. & Wilson) Lindb.	*Calomniaceae*
Calomnion laetum Hook.f. & Wilson	*Calomniaceae*
Calyptopogon mnioides (Schwägr.) Broth.	*Pottiaceae*
Camptochaete angustata (Mitt.) Reichardt	*Lembophyllaceae*
Campylopodium medium (Duby) Giese & J.-P.Frahm	*Dicranaceae*
Campylopus acuminatus var. *kirkii* (Mitt.) J.-P.Frahm	*Dicranaceae*
Campylopus bicolor (Müll.Hal.) Hook.f. & Wilson	*Dicranaceae*
Campylopus capillaceus Hook.f. & Wilson	*Dicranaceae*
Campylopus clavatus (R.Br.) Hook.f. & Wilson	*Dicranaceae*
Campylopus introflexus (Hedw.) Brid.	*Dicranaceae*
Canalohypopterygium tamariscinum (Hedw.) Kruijer	*Hypopterygiaceae*
Chrysoblastella chilensis (Mont.) Reimers	*Ditrichaceae*
Cladomnion ericoides (Hook.) Hook.f. & Wilson	*Ptychomniaceae*
Conostomum pentastichum (Brid.) Lindb.	*Bartramiaceae*
Conostomum pusillum Hook.f. & Wilson	*Bartramiaceae*
Cratoneuropsis relaxa (Hook.f. & Wilson) Broth.	*Amblystegiaceae*
Crosbya straminea (Beckett) Vitt	*Daltoniaceae*
Cryptopodium bartramioides (Hook.) Brid.	*Rhizogoniaceae*
Cyathophorum bulbosum (Hedw.) Müll.Hal.	*Hypopterygiaceae*
Dendroligotrichum dendroides (Hedw.) Broth.	*Polytrichaceae*
Dicnemon calycinum (Hook.) Schwägr.	*Dicnemonaceae*
Dicnemon dixonianum B.H.Allen	*Dicnemonaceae*
Dicnemon semicryptum Müll.Hal.	*Dicnemonaceae*
Dicranella cardotii (R.Br.bis) Dixon	*Dicranaceae*
Dicranella gracillima (Beckett) Paris	*Dicranaceae*
Dicranoloma billardierei (Brid.) Paris	*Dicranaceae*
Dicranoloma dicarpum (Nees) Paris	*Dicranaceae*

Dicranoloma fasciatum (Hedw.) Paris	*Dicranaceae*
Dicranoloma menziesii (Hook.f. & Wilson) Paris	*Dicranaceae*
Dicranoloma robustum (Hook.f. & Wilson) Paris	*Dicranaceae*
Dicranoweisia antarctica (Müll.Hal.) Paris	*Dicranaceae*
Dicranum aucklandicum Dixon	*Dicranaceae*
Distichium capillaceum (Hedw.) Bruch & Schimp.	*Ditrichaceae*
Distichophyllum crispulum (Hook.f. & Wilson) Mitt.	*Daltoniaceae*
Distichophyllum kraussei (Lorentz) Mitt.	*Daltoniaceae*
Distichophyllum pulchellum (Hampe) Mitt.	*Daltoniaceae*
Distichophyllum rotundifolium (Hook.f. & Wilson) Müll.Hal. & Broth.	*Daltoniaceae*
Ditrichum brevirostre (R.Br.bis) Broth.	*Ditrichaceae*
Ditrichum difficile (Duby) M.Fleisch.	*Ditrichaceae*
Ditrichum punctulatum Mitt.	*Ditrichaceae*
Ditrichum strictum (Hook.f. & Wilson) Hampe	*Ditrichaceae*
Drepanocladus aduncus (Hedw.) Warnst.	*Amblystegiaceae*
Drepanocladus revolvens (Sw.) Warnst.	*Amblystegiaceae*
Ephemeropsis trentepohlioides (Renner) Sainsbury	*Ephemeropsaceae*
Fissidens asplenioides Hedw.	*Fissidentaceae*
Fissidens leptocladus Rodway	*Fissidentaceae*
Fissidens pallidus Hook.f. & Wilson	*Fissidentaceae*
Fissidens pungens Müll.Hal. & Hampe	*Fissidentaceae*
Fissidens rigidulus Hook.f. & Wilson	*Fissidentaceae*
Fissidens tenellus Hook.f. & Wilson var. *tenellus*	*Fissidentaceae*
Grimmia incrassicapsulis B.G.Bell	*Grimmiaceae*
Grimmia pulvinata (Hedw.) Sm. & Sowerby	*Grimmiaceae*
Holomitrium perichaetiale (Hook.) Brid.	*Dicranaceae*
Hymenodon pilifer Hook.f. & Wilson	*Rhizogoniaceae*
Hypnodendron arcuatum (Hedw.) Mitt.	*Hypnodendraceae*
Hypnodendron colensoi (Hook.f. & Wilson) Mitt.	*Hypnodendraceae*
Hypnodendron comosum (Labill.) Mitt.	*Hypnodendraceae*
Hypnodendron menziesii (Hook.) Paris	*Hypnodendraceae*
Hypnum chrysogaster Müll.Hal.	*Hypnodendraceae*
Hypnum cupressiforme Hedw.	*Hypnodendraceae*
Leptostomum inclinans R.Br.	*Bryaceae*
Leptostomum macrocarpum (Hedw.) Bach.Pyl.	*Bryaceae*
Leptotheca gaudichaudii Schwägr.	*Rhizogoniaceae*
Lepyrodon australis Broth.	*Lepyrodontaceae*
Lepyrodon lagurus (Hook.) Mitt.	*Lepyrodontaceae*
Leucobryum candidum (P.Beauv.) Hook.f. & Wilson	*Leucobryaceae*
Lopidium concinnum (Hook.) Wilson	*Hypopterygiaceae*
Macromitrium gracile (Hook.) Schwägr.	*Orthotrichaceae*
Macromitrium longipes (Hook.) Schwägr.	*Orthotrichaceae*
Macromitrium microstomum (Hook. & Grev.) Schwägr.	*Orthotrichaceae*
Mittenia plumula (Mitt.) Lindb.	*Mitteniaceae*
Orthorrhynchium elegans (Hook.f. & Wilson) Reichardt	*Phyllogoniaceae*
Papillaria flavolimbata (Müll.Hal. & Hampe) A.Jaeger	*Meteoriaceae*
Philonotis scabrifolia (Hook.f. & Wilson) Braithw.	*Bartramiaceae*

Philonotis tenuis (Taylor) Reichardt	*Bartramiaceae*
Plagiomnium novae-zealandiae (Colenso) T.J.Kop.	*Mniaceae*
Pleuridium arnoldii (R.Br.bis) Paris	*Ditrichaceae*
Pleurophascum grandiglobum Lindb.	*Pleurophascaceae*
Pleurophascum ovalifolium Fife & P.J.Dalton	*Pleurophascaceae*
Pogonatum subulatum (Brid.) Brid.	*Polytrichaceae*
Pohlia cruda (Hedw.) Lindb.	*Bryaceae*
Pohlia wahlenbergii (F.Weber & D.Mohr) Andr.	*Bryaceae*
Polytrichadelphus magellanicus (Hedw.) Mitt.	*Polytrichaceae*
Polytrichastrum alpinum (Hedw.) Merrill	*Polytrichaceae*
Polytrichum commune Hedw.	*Polytrichaceae*
Polytrichum juniperinum Hedw.	*Polytrichaceae*
Ptychomnion aciculare (Brid.) Mitt.	*Ptychomniaceae*
Ptychomnion densifolium (Brid.) A.Jaeger	*Ptychomniaceae*
Pulchrinodus inflatus (Hook.f. & Wilson) B.H.Allen	*Pterobryaceae*
Pyrrhobryum bifarium (Hook.) Manuel	*Rhizogoniaceae*
Pyrrhobryum mnioides (Hook.) Manuel	*Rhizogoniaceae*
Racomitrium crispulum (Hook.f. & Wilson) Hook.f. & Wilson	*Grimmiaceae*
Racomitrium lanuginosum (Hedw.) Brid.	*Grimmiaceae*
Racomitrium pruinosum (Hook.f. & Wilson) Müll.Hal.	*Grimmiaceae*
Racomitrium striatipilum Cardot	*Grimmiaceae*
Racopilum convolutaceum (Müll.Hal.) Reichardt	*Racopilaceae*
Rhacocarpus purpurascens (Brid.) Paris	*Hedwigiaceae*
Rhaphidorrhynchium amoenum (Hedw.) M.Fleisch.	*Sematophyllaceae*
Rhizogonium distichum (Sw.) Brid.	*Rhizogoniaceae*
Rhizogonium novae-hollandiae (Brid.) Brid.	*Rhizogoniaceae*
Rhizogonium pennatum Hook.f. & Wilson	*Rhizogoniaceae*
Rhynchostegium tenuifolium (Hedw.) Reichardt	*Brachytheciaceae*
Schizymenium bryoides Hook.	*Bryaceae*
Sematophyllum uncinatum I.G.Stone & G.A.M.Scott	*Sematophyllaceae*
Sphagnum australe Mitt.	*Sphagnaceae*
Sphagnum cristatum Hampe	*Sphagnaceae*
Sphagnum falcatulum Besch.	*Sphagnaceae*
Syntrichia robusta (Hook. & Grev.) R.H.Zander	*Pottiaceae*
Thuidium furfurosum (Hook.f. & Wilson) Reichardt	*Thuidiaceae*
Thuidium laeviusculum (Mitt.) A.Jaeger	*Thuidiaceae*
Warnstorfia fluitans (Hedw.) Loeske	*Amblystegiaceae*
Weissia controversa Hedw.	*Pottiaceae*
Weymouthia cochlearifolia (Schwägr.) Dixon	*Meteoriaceae*
Weymouthia mollis (Hedw.) Broth.	*Meteoriaceae*
Wijkia extenuata (Brid.) H.A.Crum	*Sematophyllaceae*

Liverworts not treated in this volume

Acrobolbus cinerascens (Lehm. & Lindenb.) Bastow	*Acrobolbaceae*
Acrobolbus concinnus (Mitt.) Grolle	*Acrobolbaceae*
Acrobolbus ochrophyllus (Hook.f. & Taylor) R.M.Schust.	*Acrobolbaceae*

APPENDIX

Acrochila biserialis (Lehm. & Lindenb.) Grolle	*Plagiochilaceae*
Acrolejeunea allisonii Gradst.	*Lejeuneaceae*
Acrolejeunea mollis (Hook.f. & Taylor) Schiffn.	*Lejeuneaceae*
Allisonia cockaynei (Steph.) R.M.Schust.	*Allisoniaceae*
Aneura alterniloba (Hook.f. & Taylor) Gottsche, Lindenb. & Nees	*Aneuraceae*
Archilejeunea olivacea (Hook.f. & Taylor) Steph.	*Lejeuneaceae*
Archilejeunea planiuscula (Mitt.) Steph.	*Lejeuneaceae*
Asterella australis (Hook.f. & Taylor) Verd.	*Aytoniaceae*
Asterella tenera (Mitt.) R.M.Schust.	*Aytoniaceae*
Austrofossombronia australis (Mitt.) R.M.Schust.	*Fossombroniaceae*
Austrolejeunea conchophylla Pócs	*Lejeuneaceae*
Austrolejeunea hamata (Grolle) Pócs	*Lejeuneaceae*
Austrolejeunea olgae (R.M.Schust.) R.M.Schust.	*Lejeuneaceae*
Austrolejeunea papillosa (Glenny) Pócs	*Lejeuneaceae*
Austrolophozia paradoxa R.M.Schust.	*Acrobolbaceae*
Austrometzgeria saccata (Mitt.) Kuwah.	*Metzgeriaceae*
Austroscyphus nitidissimus (R.M.Schust.) R.M.Schust.	*Balantiopsaceae*
Balantiopsis convexiuscula Berggr.	*Balantiopsaceae*
Balantiopsis diplophylla (Hook.f. & Taylor) Mitt.	*Balantiopsaceae*
Balantiopsis tumida Berggr.	*Balantiopsaceae*
Balantiopsis verrucosa J.J.Engel & Merrill	*Balantiopsaceae*
Bragginsella anomala R.M.Schust.	*Lophocoleaceae*
Brevianthus flavus (Grolle) J.J.Engel & R.M.Schust.	*Brevianthaceae*
Chaetophyllopsis whiteleggei (Carrington & Pearson) R.M.Schust.	*Chaetophyllopsaceae*
Cheilolejeunea albovirens (Hook.f. & Taylor) E.A.Hodgs.	*Lejeuneaceae*
Cheilolejeunea campbelliensis (Steph.) R.M.Schust.	*Lejeuneaceae*
Cheilolejeunea mimosa (Hook.f. & Taylor) R.M.Schust.	*Lejeuneaceae*
Chiloscyphus austrigenus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus bispinosus (Hook.f. & Taylor) J.J.Engel & R.M.Schust	*Lophocoleaceae*
Chiloscyphus calcareus (Steph.) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus echinellus (Lindenb. & Gottsche) Mitt.	*Lophocoleaceae*
Chiloscyphus helmsianus (Steph.) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus lentus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus leucophyllus (Hook.f. & Taylor) Gottsche, Lindenb. & Nees	*Lophocoleaceae*
Chiloscyphus mittenianus (Colenso) J.J.Engel	*Lophocoleaceae*
Chiloscyphus muricatus (Lehm.) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus semiteres (Lehm.) Lehm.	*Lophocoleaceae*
Chiloscyphus spiniferus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus subporosus (Mitt.) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Chiloscyphus tuberculatus J.J.Engel	*Lophocoleaceae*
Clasmatocolea humilis (Hook.f. & Taylor) Grolle	*Lophocoleaceae*
Clasmatocolea notophylla (Hook.f. & Taylor) Grolle	*Lophocoleaceae*
Clasmatocolea strongylophylla (Hook.f. & Taylor) Grolle	*Lophocoleaceae*
Clasmatocolea vermicularis (Lehm.) Grolle	*Lophocoleaceae*
Cololejeunea cardiocarpa (Mont.) R.M.Schust.	*Lejeuneaceae*

Cololejeunea falcidentata R.M.Schust.	*Lejeuneaceae*
Cololejeunea hodgsoniae (Herzog) E.A.Hodgs.	*Lejeuneaceae*
Cololejeunea pulchella (Mitt.) R.M.Schust.	*Lejeuneaceae*
Colura pulcherrima Ast	*Lejeuneaceae*
Colura saccophylla E.A.Hodgs. & Herzog	*Lejeuneaceae*
Cryptostipula R.M.Schust.	*Jungermanniaceae*
Dendromastigophora flagellifera (Hook.f.) R.M.Schust.	*Mastigophoraceae*
Diplasiolejeunea plicatiloba (Hook.f. & Taylor) Grolle	*Lejeuneaceae*
Diplophyllum domesticum (Gottsche) Steph.	*Scapaniaceae*
Drepanolejeunea aucklandica Steph.	*Lejeuneaceae*
Dumortiera hirsuta (Sw.) Nees	*Marchantiaceae*
Echinolejeunea papillata (Mitt.) R.M.Schust.	*Lejeuneaceae*
Eoisotachis stephanii (Salm.) R.M.Schust.	*Balantiopsaceae*
Fossombronia pusilla (L.) Nees	*Fossombroniaceae*
Fossombronia wondraczekii (Corda) Dumort.	*Fossombroniaceae*
Frullania aterrima (Hook.f. & Taylor) Hook.f. & Taylor	*Frullaniaceae*
Frullania chevalieri (R.M.Schust.) R.M.Schust.	*Frullaniaceae*
Frullania deplanata Mitt.	*Frullaniaceae*
Frullania monocera (Hook.f. & Taylor) Gottsche, Lindenb. & Nees	*Frullaniaceae*
Frullania patula Mitt.	*Frullaniaceae*
Frullania rostrata (Hook.f. & Taylor) Hook.f. & Taylor	*Frullaniaceae*
Frullania setchellii Pearson	*Frullaniaceae*
Gackstroemia alpina R.M.Schust.	*Lepidolaenaceae*
Gackstroemia weindorferi (Herzog) Grolle	*Lepidolaenaceae*
Geocalyx caledonicus Steph.	*Geocalycaceae*
Goebeliella cornigera (Mitt.) Steph.	*Goebeliellaceae*
Goebelobryum unguiculatum (Hook.f. & Taylor) Grolle	*Acrobolbaceae*
Harpalejeunea filicuspis (Steph.) Mizut.	*Lejeuneaceae*
Harpalejeunea latitans (Hook.f. & Taylor) Grolle	*Lejeuneaceae*
Hepatostolonophora paucistipula (Rodway) J.J.Engel	*Lophocoleaceae*
Hepatostolonophora rotata var. *perssonii* (R.M.Schust.) J.J.Engel	*Lophocoleaceae*
Herzogianthus sanguineus R.M.Schust.	*Chaetophyllopsaceae*
Herzogianthus vaginatus (Herzog) R.M.Schust.	*Chaetophyllopsaceae*
Heteroscyphus billardierei (Schwägr.) Schiffn.	*Lophocoleaceae*
Heteroscyphus coalitis (Hook.) Schiffn.	*Lophocoleaceae*
Heteroscyphus cuneistipulus (Steph.) Schiffn.	*Lophocoleaceae*
Heteroscyphus cymbaliferus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Heteroscyphus decipiens (Gottsche) J.J.Engel & R.M.Schust.	*Lophocoleaceae*
Heteroscyphus mononuculus J.J.Engel	*Lophocoleaceae*
Heteroscyphus sinuosus (Hook.) Schiffn.	*Lophocoleaceae*
Heteroscyphus triacanthus (Hook.f. & Taylor) Schiffn.	*Lophocoleaceae*
Hymenophyton flabellatum (Labill.) Trevis.	*Hymenophytaceae*
Hymenophyton leptopodum (Hook.f. & Taylor) A.Evans	*Hymenophytaceae*
Isotachis intortifolia (Hook.f. & Taylor) Gottsche	*Balantiopsaceae*
Isotachis lyallii Mitt.	*Balantiopsaceae*
Isotachis montana Colenso	*Balantiopsaceae*

Isotachis olivacea R.M.Schust.	*Balantiopsaceae*
Isotachis plicata J.J.Engel	*Balantiopsaceae*
Jensenia connivens (Colenso) Grolle	*Pallaviciniaceae*
Kymatolejeunea bartlettii Grolle	*Lejeuneaceae*
Lamellocolea granditexta (Steph.) J.J.Engel	*Lophocoleaceae*
Lejeunea cyanophora R.M.Schust.	*Lejeuneaceae*
Lejeunea flava (Sw.) Nees	*Lejeuneaceae*
Lejeunea primordialis (Hook.f. & Taylor) Gottsche, Lindenb. & Nees	*Lejeuneaceae*
Lejeunea tumida Mitt.	*Lejeuneaceae*
Lepidogyna hodgsoniae (Grolle) R.M.Schust.	*Lepidolaenaceae*
Lepidolaena berggrenii E.A.Hodgs.	*Lepidolaenaceae*
Lepidolaena clavigera (Hook.) Trevis.	*Lepidolaenaceae*
Lepidolaena palpebrifolia (Hook.) Trevis.	*Lepidolaenaceae*
Lepidolaena reticulata (Hook.f. & Taylor) Trevis.	*Lepidolaenaceae*
Lepidolaena taylorii (Gottsche) Trevis.	*Lepidolaenaceae*
Leptolejeunea elliptica (Lehm. & Lindenb.) Steph.	*Lejeuneaceae*
Leptoscyphus australis (Hook.f. & Taylor) R.M.Schust.	*Lophocoleaceae*
Lethocolea pansa (Taylor) G.A.M.Scott & K.Beckmann	*Acrobolbaceae*
Lopholejeunea colensoi Steph.	*Lejeuneaceae*
Lunularia cruciata (L.) Dumort.	*Lunulariaceae*
Maculia filosa E.A.Hodgs.	*Lepidoziaceae*
Marchantia berteroana Lehm. & Lindenb.	*Marchantiaceae*
Marchantia foliacea Mitt.	*Marchantiaceae*
Marchantia macropora Mitt.	*Marchantiaceae*
Marchantia pileata Mitt.	*Marchantiaceae*
Marchantia polymorpha L.	*Marchantiaceae*
Marsupidium epiphytum Colenso	*Acrobolbaceae*
Marsupidium knightii Mitt.	*Acrobolbaceae*
Marsupidium surculosum (Nees) Schiffn.	*Acrobolbaceae*
Mastigolejeunea anguiformis (Hook.f. & Taylor) B.Thiers & Gradst.	*Lejeuneaceae*
Metzgeria atrichoneura Spruce	*Metzgeriaceae*
Metzgeria decipiens (C.Massal.) Schiffn.	*Metzgeriaceae*
Metzgeria flavovirens Colenso	*Metzgeriaceae*
Metzgeria furcata (L.) Dumort.	*Metzgeriaceae*
Metzgeria leptoneura Spruce	*Metzgeriaceae*
Metzgeria rigida Lindb.	*Metzgeriaceae*
Metzgeria scobina Mitt.	*Metzgeriaceae*
Metzgeria submarginata M.L.So	*Metzgeriaceae*
Monoclea forsteri Hook.	*Monocleaceae*
Neohodgsonia mirabilis (Perss.) Perss.	*Marchantiaceae*
Pachyglossa tenacifolia (Hook.f. & Taylor) Herzog & Grolle	*Lophocoleaceae*
Pachyschistochila altissima (E.A.Hodgs.) R.M.Schust.	*Schistochilaceae*
Pachyschistochila berggrenii J.J.Engel & R.M.Schust.	*Schistochilaceae*
Pachyschistochila childii R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pachyschistochila colensoana (Steph.) R.M.Schust. & J.J.Engel	*Schistochilaceae*

Pachyschistochila nivicola R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pachyschistochila papillifera (R.M.Schust.) R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pachyschistochila parvistipula (Rodway) R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pachyschistochila subhyalina (R.M.Schust.) R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pachyschistochila succulenta J.J.Engel & R.M.Schust.	*Schistochilaceae*
Pachyschistochila trispiralis (R.M.Schust.) R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pachyschistochila virescens (R.M.Schust.) R.M.Schust. & J.J.Engel	*Schistochilaceae*
Pallavicinia innovans Steph.	*Pallaviciniaceae*
Pallavicinia rubristipa Schiffn.	*Pallaviciniaceae*
Pallavicinia tenuinervis (Hook.f. & Taylor) Trevis.	*Pallaviciniaceae*
Pallavicinia xiphoides (Hook.f. & Taylor) Trevis.	*Pallaviciniaceae*
Paraschistochila conchophylla (E.A.Hodgs. & Allison) R.M.Schust.	*Schistochilaceae*
Paraschistochila pinnatifolia (Hook.) R.M.Schust.	*Schistochilaceae*
Paraschistochila tuloides (Hook.f. & Taylor) R.M.Schust.	*Schistochilaceae*
Pedinophyllum monoicum (Steph.) Grolle	*Plagiochilaceae*
Petalophyllum hodgsoniae Crandall-Stolter & C.H.Ford	*Fossombroniaceae*
Phyllothallia nivicola E.A.Hodgs.	*Phyllothalliaceae*
Plagiochasma rupestre (J.R.Forst. & G.Forst.) Steph.	*Aytoniaceae*
Plagiochila annotina Lindenb.	*Plagiochilaceae*
Plagiochila baileyana Steph.	*Plagiochilaceae*
Plagiochila banksiana Gottsche	*Plagiochilaceae*
Plagiochila bazzanioides J.J.Engel & Merrill	*Plagiochilaceae*
Plagiochila caducifolia Inoue & R.M.Schust.	*Plagiochilaceae*
Plagiochila circinalis (Lehm. & Lindenb.) Lehm. & Lindenb.	*Plagiochilaceae*
Plagiochila deltoidea Lindenb.	*Plagiochilaceae*
Plagiochila fasciculata Lindenb.	*Plagiochilaceae*
Plagiochila fuscella (Hook.f. & Taylor) Taylor & Hook.f.	*Plagiochilaceae*
Plagiochila gigantea Lindenb.	*Plagiochilaceae*
Plagiochila hatcheri J.J.Engel & Merrill	*Plagiochilaceae*
Plagiochila incurvicolla (Hook.f. & Taylor) Hook.f. & Taylor	*Plagiochilaceae*
Plagiochila intertexta Hook.f. & Taylor	*Plagiochilaceae*
Plagiochila kermadecensis J.J.Engel & Merrill	*Plagiochilaceae*
Plagiochila lyallii Mitt.	*Plagiochilaceae*
Plagiochila obscura Colenso	*Plagiochilaceae*
Plagiochila pacifica Mitt.	*Plagiochilaceae*
Plagiochila radiculosa Mitt.	*Plagiochilaceae*
Plagiochila ramosissima (Hook.) Lindenb.	*Plagiochilaceae*
Plagiochila retrospectans (Nees) Nees	*Plagiochilaceae*
Plagiochila rutlandii Steph.	*Plagiochilaceae*
Plagiochila stephensoniana Mitt.	*Plagiochilaceae*
Plagiochila strombifolia Taylor	*Plagiochilaceae*
Plagiochila subsimilis Colenso	*Plagiochilaceae*

Plagiochilion conjugatum (Hook.) R.M.Schust.	*Plagiochilaceae*
Plagiochilion prolifer (Mitt.) R.M.Schust.	*Plagiochilaceae*
Podomitrium phyllanthus (Hook.) Mitt.	*Pallaviciniaceae*
Porella elegantula (Mont.) E.A.Hodgs.	*Porellaceae*
Pseudolophocolea denticulata R.M.Schust. & J.J.Engel	*Lophocoleaceae*
Ptilidium ciliare (L.) Hampe	*Ptilidiaceae*
Radula buccinifera (Hook.f. & Taylor) Gottsche, Lindenb. & Nees	*Radulaceae*
Radula cordiloba Taylor	*Radulaceae*
Radula dentifolia Grolle	*Radulaceae*
Radula grandis Steph.	*Radulaceae*
Radula marginata Taylor *ex* Gottsche, Lindenb. & Nees	*Radulaceae*
Radula papulosa Steph.	*Radulaceae*
Radula parviretis E.A.Hodgs.	*Radulaceae*
Radula physoloba Mont.	*Radulaceae*
Radula pseudoscripta M.A.M.Renner	*Radulaceae*
Radula ratkowskiana K.Yamada	*Radulaceae*
Radula sainsburiana E.A.Hodgs. & Allison	*Radulaceae*
Radula scariosa Mitt.	*Radulaceae*
Radula silvosa E.A.Hodgs. & Allison	*Radulaceae*
Radula tasmanica Steph.	*Radulaceae*
Reboulia hemisphaerica (L.) Raddi	*Aytoniaceae*
Rectolejeunea denudata R.M.Schust.	*Lejeuneaceae*
Riccardia aequicellularis (Steph.) Hewson	*Aneuraceae*
Riccardia aequitexta (Steph.) E.A.Brown	*Aneuraceae*
Riccardia alcicornis (Hook.f. & Taylor) Trevis.	*Aneuraceae*
Riccardia australis (Hook.f. & Leveille) E.A.Brown	*Aneuraceae*
Riccardia bipinnatifida (Colenso) Hewson	*Aneuraceae*
Riccardia cochleata (Hook.f. & Taylor) Kuntze	*Aneuraceae*
Riccardia colensoi (Steph.) W.Martin	*Aneuraceae*
Riccardia crassa (Schwägr.) C.Massal.	*Aneuraceae*
Riccardia furtiva E.A.Brown & Braggins	*Aneuraceae*
Riccardia intercellula E.A.Brown	*Aneuraceae*
Riccardia multicorpora E.A.Brown	*Aneuraceae*
Riccardia pallidevirens (Steph.) A.Evans	*Aneuraceae*
Riccardia pennata E.A.Brown	*Aneuraceae*
Riccardia perspicua E.A.Brown	*Aneuraceae*
Riccardia pseudodendroceros R.M.Schust.	*Aneuraceae*
Riccardia pusilla (Steph.) E.A.Brown	*Aneuraceae*
Riccardia umida E.A.Brown	*Aneuraceae*
Riccia bifurca Hoffm.	*Ricciaceae*
Riccia bullosa Link	*Ricciaceae*
Riccia ciliata Hoffm.	*Ricciaceae*
Riccia crozalsii Levier	*Ricciaceae*
Riccia crystallina L.	*Ricciaceae*
Riccia fluitans L.	*Ricciaceae*
Ricciocarpos natans (L.) Corda	*Ricciaceae*
Saccogynidium australe (Mitt.) Grolle	*Geocalycaceae*
Saccogynidium decurvum (Mitt.) Grolle	*Geocalycaceae*

Schistochila appendiculata (Hook.) Trevis.	*Schistochilaceae*
Schistochila balfouriana (Hook.f. & Taylor) Steph.	*Schistochilaceae*
Schistochila chlorophylla (Colenso) J.J.Engel & R.M.Schust.	*Schistochilaceae*
Schistochila ciliata (Mitt.) Steph.	*Schistochilaceae*
Schistochila glaucescens (Hook.) A.Evans	*Schistochilaceae*
Schistochila kirkiana Steph.	*Schistochilaceae*
Schistochila lehmanniana (Lindenb.) Carrington & Pearson	*Schistochilaceae*
Schistochila monticola R.M.Schust.	*Schistochilaceae*
Schistochila nitidissima R.M.Schust.	*Schistochilaceae*
Schistochila nobilis (Hook.) Trevis.	*Schistochilaceae*
Schistochila pellucida R.M.Schust. & J.J.Engel	*Schistochilaceae*
Schistochila pluriciliata R.M.Schust. & J.J.Engel	*Schistochilaceae*
Schistochila pseudociliata R.M.Schust.	*Schistochilaceae*
Seppeltia succuba Grolle	*Pallaviciniaceae*
Siphonolejeunea nudipes (Hook.f. & Taylor) Herzog	*Lejeuneaceae*
Stenolejeunea acuminata R.M.Schust.	*Lejeuneaceae*
Symphyogyna hymenophyllum (Hook.) Mont. & Nees	*Pallaviciniaceae*
Symphyogyna subsimplex Mitt.	*Pallaviciniaceae*
Symphyogyna undulata Colenso	*Pallaviciniaceae*
Treubia lacunosa (Colenso) Prosk.	*Treubiaceae*
Treubia pygmaea R.M.Schust.	*Treubiaceae*
Tylimanthus diversifolius E.A.Hodgs.	*Acrobolbaceae*
Tylimanthus saccatus (Hook.) Mitt.	*Acrobolbaceae*
Tylimanthus tenellus (Taylor) Mitt.	*Acrobolbaceae*
Verdoornia succulenta R.M.Schust.	*Verdoorniaceae*
Xenothallus vulcanicolus R.M.Schust.	*Pallaviciniaceae*

Lichens

Baeomyces heteromorphus Nyl. *ex* C.Bab. & Mitt.	*Baeomycetaceae*
Bunodophoron scrobiculatum (C.Bab.) Wedin	*Sphaerophoraceae*
Cladia aggregata (Sw.) Nyl.	*Cladoniaceae*
Cladia retipora (Labill.) Nyl.	*Cladoniaceae*
Cladonia confusa R.Sant.	*Cladoniaceae*
Dibaeis arcuata (Stirt.) Kalb & Gierl	*Icmadophilaceae*
Leifidium tenerum (Laurer) Wedin	*Sphaerophoraceae*
Menegazzia pertransita (Stirt.) R.Sant.	*Parmeliaceae*
Porina exocha (Nyl.) P.M.McCarthy	*Porinaceae*
Pseudocyphellaria multifida (Nyl.) D.J.Galloway & P.James	*Lobariaceae*
Rhizocarpon geographicum (L.) DC.	*Rhizocarpaceae*
Siphula decumbens Nyl.	*Incert. sed.*
Siphula fragilis (Hook.f. & Taylor) J.S.Murray	*Incert. sed.*
Solorina crocea (L.) Ach.	*Peltigeraceae*
Stereocaulon ramulosum Raeusch.	*Stereocaulaceae*
Sticta filix (Sw.) Nyl.	*Lobariaceae*
Usnea contexta Motyka	*Parmeliaceae*
Usnea rubicunda Stirt.	*Parmeliaceae*

GLOSSARY

abaxial: facing away from the axis or central axis (the opposite is adaxial).

accessory lobe: a large tooth that is nearly the size of the adjacent leaf lobes, usually on the leaf or underleaf disc margin (e.g., *Kurzia hippuroides*, Fig. 79: 7).

***Acromastigum*-type branch**: terminal branch that replaces half of an underleaf and originates from either half of a ventral merophyte segment (e.g., *Acromastigum colensoanum*, Fig. 87: 5).

aculeate (surface of spores, leaves, thallus): ornamentation one per cell, radially symmetric, no higher than wide, broadly attached and tapering to an acute apex; e.g., spores of *Lepicolea attenuata* (Fig. 6: 9).

acuminate: gradually terminating to a point; bounded by lines changing from straight or convex to concave and converging gradually to a point (e.g., *Cuspidatula monodon*, Fig. 159: 1).

adaxial: facing toward the axis or central axis (the opposite is abaxial).

alternate (arrangement of leaves): staggered on the two sides of a stem rather than exactly opposite each other (e.g., *Solenostoma hodgsoniae*, Fig. 153: 1). Cf. opposite.

amphi-Atlantic: occurring on land masses on both eastern and western sides of the Atlantic Ocean.

amphi-Pacific: occurring on land masses on both eastern and western sides of the Pacific Ocean.

amplexicaul (leaf base): clasping the stem (e.g., *Diplophyllum verrucosum*, Fig. 164: 3).

ampliate (margin): enlarged, outwardly curved; e.g., dorsal margin of *Lepidozia setigera* leaves.

ampliation: enlargement, especially of the margin of a leaf relative to the other margin.

anastomosing: a joined network like a system of blood vessels.

***Andrewsianthus*-type branch**: lateral-intercalary branch arising from the dorsal-lateral side of the stem; the branch originates from the antical part of the lateral segment (the branch type is a generic character for the genus *Andrewsianthus*).

androecium (plural: **androecia**): site of male reproduction, including protective scales or leaves (bracts) and the antheridia (e.g., *Telaranea inaequalis*, Fig. 78: 15).

-androus: with antheridia, e.g., a 1–2-androus bract has either one or two antheridia.

anisophyllous (plants): having underleaves different in size and shape from the lateral leaves, always smaller. Cf. isophyllous.

antheridia (singular: **antheridium**): sacs in which the male sperm or spermatozoids develop. They are spherical or ellipsoidal, stalked, usually yellow or whitish, and usually found in the axils of male bracts—modified leaves that are usually smaller and more concave than vegetative leaves (e.g., *Solenostoma hodgsoniae*, Plate 13G).

antical: facing toward the apex of a plant. Usually used to refer to the margin of a (obliquely or longitudinally inserted) leaf that is nearest to the shoot apex. Cf. postical.

apical (of a plant, shoot, stem, leaf, etc.): at the end farthest from the base or point of attachment. Cf. basal.

apiculate: ending abruptly in a short, sharp tip (cuspidate is longer and stouter) (e.g., *Diplophyllum domesticum*, Fig. 167: 2).

appendiculate (margins): bearing small appendages, e.g., with laciniae.

appendiculi: appendages, such as laciniae, on a leaf or bract margin or at a leaf base.

appressed (leaves): flattened or pressed against the stem with no gap between the two. Cf. oblique, patent, subsquarrose, squarrose.

approximate/approximated (leaf arrangement): close together but not touching or overlapping.

arbuscules: much-branched, microscopic haustorial structures of glomeromycote fungal symbionts that form within the host plant's cells. The interface between arbuscules and the plant plasma membrane is the main site of exchange of nutrients and growth-regulating chemicals (e.g., Fig. 2a).

archegonium (plural: **archegonia**): flask-shaped structure in the gynoecium consisting of a long neck and a venter that holds the egg. When the egg is fertilized, it develops it into the embryonic sporophyte.

arcuate: curved like a bow.

area apicularis: the part of a leaf directly below the apex, especially where the cells differ from those in the middle or basal portion.

area basalis: the base of a leaf, especially when the cells differ from those in the rest of the leaf.

areolate (spores): an angular or polyhedral space marked on a surface by ridges and forming a network (e.g., *Telaranea* spp., *Riccia* spp.).

areolation (leaves): the cellular network of a leaf or thallus; usually in reference to a pattern.

armature: collective term for projections from leaf, stem or thallus surfaces.

armed: with projections from the leaf, stem or thallus surface.

ascomycete: a member of the fungal division *Ascomycota* that produce spores in a sac called an ascus. The fungal partner of most lichens is an ascomycete.

asexual reproduction: a means of establishing new plants without the usual meiosis or fusion of gametes, using parts that break off the parent plant. For example, leaf lobes can fragment easily in some species, or specialized cells or groups of cells (gemmae) develop on leaf margins, or on leaf or thallus surfaces (e.g., leaf lobe fragmentation in *Lepidozia fugax*, Fig. 39: 1, 4, 5; entire leaves of *Bazzania nova*, Fig. 99: 6).

asperulate: with a finely roughened texture, with tiny orbicular to short linear markings, lending a speckled appearance, e.g., *Cryptochila grandiflora*.

assurgent: pointing upward, or slanting upward.

athecal: without a collar or sheath of tissue; said of branches with an exogenous origin, e.g., *Frullania*-type terminal branching.

attenuate (of stems, shoots or leaf lobes): tapering gradually toward the apex (e.g., *Lepidozia acantha*, Fig. 41: 7).

auriculate (leaves, underleaves): with an ear-like appendage; usually present at the leaf or underleaf base (e.g., *Lepidozia glaucophylla*, Fig. 47: 3, 4).

Austral: used synonymously with south temperate–subantarctic. Cf. south temperate.

autoecious (noun: **autoecy**): producing androecia and gynoecia on the same plant (a type of monoecy) but on different branches (e.g., *Lophozia monoica*, Fig. 141: 1). Cf. paroecious.

awn: an abrupt, stiff, straight, subulate, hair-like point of various lengths.

axenic (culture): free of contaminating organisms, a pure culture of a single species.

axis: main stem of a leafy plant. Less often as the imaginary, longitudinal line that runs the length of a stem or shoot, or that divides a structure such as a leaf into more or less equal halves.

baculate (surface of spores, leaves): ornamentation at least 1.5× longer than wide, typically cylindrical, rod-shaped, e.g., on the leaf surface of *Acrobolbus cinerascens*, the spore surface of *Herbertus oldfieldianus* (Fig. 12: 7). A single rod-shaped ornament is a baculum (plural bacula).

basal: at the base (of a plant, stem, shoot, leaf, etc.) Cf. apical.

basidiomycete: a member of the fungal division *Basidiomycota* that includes species that produce spores in a sac called a basidium, and includes gilled fungi.
basiscopic: at or near the base of a structure.
basitonic: branching particularly well developed near the base of the stem or innovation.
bifid: divided in two, the parts not necessarily equal in size (e.g., leaves of *Telaranea inaequalis*, Fig. 78: 4).
bifurcate: divided in two, equally (e.g., leaves of *Telaranea quinquespina*, Fig. 74: 6).
bilabiate: shallowly divided into two lip-like lobes (e.g., the perianth summit of *Leptoscyphus*).
bilaterally flattened, compressed: flattened so as to appear widest when viewed from the side, e.g., perianths of *Leptoscyphus*. Cf. dorsiventrally flattened.
bipinnate (branching): with both primary and secondary axes pinnate; having pinnae that themselves have short side branches (e.g., *Lepidozia spinosissima*, Fig. 29: 1 and Plate 6C).
bipolar: found in temperate to Arctic regions in the north and in Antipodal regions, but not between.
bisbifid: divided into four lobes with the middle sinus deeper than the outer two sinuses (e.g., leaves of *Lepicolea scolopendra*, Fig. 7: 7).
biseriate: of cells arranged in two vertical rows; applied to a condition of antherial stalks or of protracted leaf or underleaf lobes (e.g., antheridial stalk of *Anthelia juratzkana*, Fig. 125: 11).
bisexual: with both sexes represented on one plant, i.e., monoecious.
bispiral (elaters): with two spiraled thickening bands (e.g., *Chandonanthus squarrosus*, Fig. 139: 6).
bistratose: composed of two layers of cells (e.g., capsule walls of *Telaranea herzogii*, Fig. 76: 7; leaves of *Anthelia juratzkana*, Fig. 125: 5, 6).
boreal: the circumpolar bioclimatic zone of the Northern Hemisphere, especially in reference to the zone with coniferous forests.
botryoidal (oil-bodies): like a cluster of grapes (see p. 46: F–H).
bract: a modified leaf that is associated with a site of reproduction, whether it be the gynoecium or androecium (e.g., *Herbertus oldfieldianus*, Fig. 11: 3).
bracteole: a modified underleaf that is associated with a site of reproduction (e.g., *Herbertus oldfieldianus*, Fig. 11: 1).
bractlet: very small bracts sometimes found next to the perianth; they are smaller than normal bracts or bracteoles.
branch half-leaf: the half of a leaf that remains when a terminal branch forms from the half of the lateral-merophyte in place of the other half of the leaf in *Frullania*- and *Microlepidozia*-type branching (e.g., *Telaranea tridactylis*, Fig. 53: 1). It is positioned at the branch junction.
caducous: breaking off; usually in reference to leaf tips or entire leaves, which may serve as vegetative propagules (e.g., leaf lobes of *Telaranea tuberifera*, Fig. 64: 5, 7; leaves of *Bazzania nova*, Fig. 99: 6).
caespitose: tufted; plants grouped and growing in cushions or tufts.
calyptra: a thin sheath that covers the developing sporophyte (capsule and seta) that is formed from the archegonial venter and neck subsequent to fertilization, rupturing distally by protrusion of the sporophyte and remaining near the base of the seta (e.g., *Pseudomarsupidium piliferum*, Fig. 130: 1).
canaliculate (leaves, bracts): channeled, the channel with a rounded (not a sharp) keel (e.g., *Blepharidophyllum vertebrale*, Fig. 174: 3).
capitate: knob-like.
capsule: a spherical, ellipsoidal or linear sporangium or sac that contains spores (e.g., *Chan-*

donanthus squarrosus, Fig. 139: 1). It is usually deep reddish brown when ripe, on a transparent or white fragile stalk.

castaneous: chestnut colored, a yellow-brown color.

caudate (lobes at leaf or underleaf apex or at perianth mouth): markedly acuminated, so that the point is elongated, like the tail of a mammal.

caudex (plural: **caudices**): tree-fern trunk.

cell lumen: see lumen.

ceraceous: the color of beeswax, a golden color.

cernuous: nodding or drooping.

chiloscyphoid: resembling *Chiloscyphus*, i.e., prostrate with succubous leaves that are usually bifid but otherwise untoothed.

chlorophyllous: cells or tissue containing chlorophyll and therefore appearing green.

chloroplast: the organelle inside the plant cell in which photosynthesis takes place. In the liverworts, chloroplasts are green, spherical, about 5 μm in diameter, and are without any discernible texture; they occur in numbers of about 10–20 per cell (e.g., *Trichotemnoma corrugatum*, Fig. 124: 3).

cilia (singular: **cilium**): single-celled or multi-celled fine hairs, often comprised of elongated cells; in *Jungermanniales* at the margin or summit of leaf or underleaf lamina or at perianth mouth (e.g., *Clandarium xiphophyllum*, Fig. 172: 4).

ciliate: fringed with fine hairs resembling the eyelash. Cf. laciniate.

cladia (singular: **cladium**): small branches that break off, acting as a form of asexual reproduction (q.v.).

clavate: club-shaped, elongate and widest near the apex.

cleared: tissue treated with a chemical agent that destroys pigments.

cnemis: an elongated convex fold resulting from decurving of the dorsal margin of a leaf, most notably in many *Plagiochila* species.

cochleariform: concave like a spoon, spoon-like.

coelocaule: a specialized shoot calyptra characterized by extreme axial proliferation and elongation simulating complete penetration of the sporophyte into the shoot apex and serving as a sporophyte protective device; associated with complete absence of a perianth (e.g., *Lepicolea*) or with incomplete or complete fusion of bracts and bracteole (e.g., *Trichocolea mollissima*, Fig. 26: 2; *Leiomitra lanata*, Fig. 23: 2) or with a low perianth at the summit of the coelocaule (e.g., *Pachyschistochila subhyalina*, cf. Schuster and Engel, 1985, fig. 67: 16).

collenchymatous: with cell walls thickened at the angles, i.e., with trigones.

complanate (shoot, branch): flattened into one plane.

conchiform: shaped like a shell (e.g., leaves of *Isolembidium anomalum*, Fig. 111: 2).

conduplicate: leaves that are folded so sharply that both halves lie in the same plane.

conduplicate-bilobed: with the lobes sharply folded together, the dorsal lobe lying over the ventral lobe or lobule, the fold rounded or keeled (e.g., *Diplophyllum verrucosum*, Fig. 164: 4).

confluent (trigones): merging, adjacent trigones not separated by a thin-walled portion of the cell wall.

connate (of an underleaf and adjacent lateral leaf or of opposing leaves fused dorsally): joined by a bridge of leafy tissue. Connate on one side indicates that an underleaf is joined to one adjacent, lateral leaf; connate on both sides indicates that it is joined to both adjacent, lateral leaves (e.g., *Bazzania novae-zelandiae*, Fig. 98: 9).

connivent: converging or pointed toward one another but not fused; usually referring to leaf lobes oriented toward one another (e.g., *Anastrophyllum schismoides*, Fig. 147: 9).

contiguous (leaves): touching but not overlapping.
convolute (leaves or bracts): rolled up, producing a spiral in cross section, either individually or one within another.
cordate (of leaves or perianths): heart-shaped (in the sense of playing cards); said of leaf shape that is rounded at base near insertion; or with reference to an appendage at the apex of a perianth.
cortex: outer layer of cells of the stem, often thick-walled to stiffen the stem. Cf. medulla.
corticolous: growing on bark of trees or shrubs.
cosmopolitan: distributed throughout the world.
crenate (margin): having rounded teeth, scalloped.
crenulate (margin): having small rounded teeth; finely scalloped.
crescentic (oil-bodies): narrowly ellipsoidal and curved, having the figure of a crescent.
crispate (leaf margin): strongly and irregularly wavy, excessively undulate; curled, twisted.
cucullate: hooded at the apex and hood-shaped.
cuneate: wedge-shaped.
cuneiform: shaped like a narrow, upside-down triangle, narrowly obtriangular.
cupulate: resembling a small cup.
cuspidate: ending abruptly in a stout rigid point (cf. apiculate).
cuticle: a term often used for the outer leaf cell surface of liverworts, but since the cell walls are not cutinized in liverworts, i.e., they lack a waxy layer, this term is not used here.
decolorate: unpigmented, hyaline.
decorticated: of a dead tree trunk or branch from which the bark has decayed and fallen away.
decurrent (leaf base): extending in an angular, usually narrow strip of tissue along the stem (e.g., *Calypogeia sphagnicola*, Fig. 121: 4).
deflexed: curved downward.
dehisce (capsule): to break apart, to open, especially along regular lines of weakness (e.g., *Metahygrobiella drucei*, Fig. 127: 1).
dehiscence: manner of splitting open of a capsule.
dendroid/dendritic: tree-like in structure, i.e., with an erect trunk-like main stem with branches mostly confined to the upper part of the plant (e.g., *Isolembidium anomalum*, Fig. 111: 1).
dentate (lamina, bract/bracteole margin): toothed, the teeth not angled.
denticulate (lamina, bract/bracteole margin): finely toothed.
determinate (branch or axis): limited in extent, especially used here in reference to growth in the sterile condition; also used in reference to a gynoecium or androecium terminating an axis and preventing its further extension.
diad (spores): a pair of spores joined on a single inner face.
dichotomous branching: terminal branching in which both branches are at an equal angle to the stem or thallus below; they are often also of subequal length (e.g., *Bazzania hochstetteri*, Fig. 97: 6).
dimorphic: occurring in two forms, e.g., leaf cells, oil-bodies.
dioecious (noun: **dioecy**): producing antheridia and archegonia on separate plants (e.g., *Bazzania adnexa*, Fig. 95: 3 and 7 showing male and female plants respectively). Usually constant for a species. Most liverworts are dioecious. The opposite state is monoecious.
disc (of a lobed leaf): the undivided part of the leaf below the lobes, akin to the palm of the hand below the fingers.
distal: toward the apical part of a shoot or leaf. Cf. proximal.
distant (leaves): not touching or overlapping those adjacent on the same side of the stem; clearly separated from each other. Cf. remote, contiguous.

distichous (leaves): arranged in two ranks on opposite sides of a stem. Usually used in leafy liverworts to refer to the leaf arrangement in those taxa with underleaves reduced or lacking.

divergent: spreading from each other, e.g., of leaf or underleaf lobes spreading from one each rather than parallel to one another (e.g., *Bazzania monilinervis*, Fig. 102: 6).

dolipore septum: the characteristic septum of basidiomycete hypha comprising a barrel-shaped structure around a central pore (Fig. 3c).

dorsal: upper aspect of a prostrate shoot. Cf. ventral.

dorsally assurgent (leaves): curved upward, the bulk of leaf lamina lies above the dorsal stem surface. Note: such leaves are usually also vertical or subvertical, although not necessarily so (e.g., *Tritomaria exsecta*, Fig. 145: 1).

dorsiventrally flattened or compressed: flattened so as to be widest when viewed from above or below; e.g., perianths of *Radula*. Cf. bilaterally flattened.

ecarinate: without a keel.

echlorophyllose: without chlorophyll; used in reference to an area of leaf (usually a border) composed of non-living cells; the area is commonly hyaline (e.g., *Herzogobryum teres*, Plate 16B).

elater: elongate cell resembling coiled springs which are present in almost all liverwort and hornwort capsules, mixed with the spores (e.g., *Chandonanthus squarrosus*, Fig. 139: 6). Elaters help to eject the spores from the capsule by a hygroscopic action.

emarginate: having a notch at the apex, indented with an acute sinus; cf. retuse in which the sinus is rounded.

emergent (perianth, capsule): partially exposed; referring to perianth or capsule only partly visible beyond the tips of gynoecial bracts or perianth mouth, respectively (e.g., *Diplophyllum dioicum*, Fig. 166: 10). Cf. exserted.

endemic: confined to a limited geographical or floristic area.

endogenous: originating from internal rather than superficial cells or tissues, e.g., of endogenous branches derived from subcortical cells.

entally displaced (hyaline papilla in *Lejeuneaceae*): situated on the interior surface of the lobule rather than on the lobule margin, so that it can be seen clearly only by dissecting the lobule.

entire (margin): lacking any teeth, indentations or erosions, ± smooth (but an entire-margined leaf may be lobed as in the leaves of *Herbertus oldfieldianus*, Fig. 11: 2).

ephemeral: short-lived.

epiphyll (epiphyllic): growing on leaves, fern fronds or moss leaves.

epiphyte (epiphytic): growing on bark, i.e. the trunk, branches or twigs of trees and shrubs.

eplicate: without plicae (q.v.).

erect: of shoots oriented perpendicularly to substrate or to a horizontal stem; of leaves when apex is directed nearly to the shoot apex.

erose: irregularly notched or ragged, indented; as if gnawed.

etiolated: as if grown in the dark, pale with stems and small distant leaves.

exogenous: originating from external cells or parts of cells; of a terminal branch potentially originating from a cortical cell (especially in *Calobryales*); of a gemma budded off from a leaf cell.

explanate: flattened, usually in reference to a lobule (especially in *Frullania*) that has not developed into a sac but appears as a flat leaf lobe.

exserted (perianth, capsule): completely visible beyond the gynoecial bracts (e.g., the perianth of *Jamesoniella colorata* in Fig. 157: 8), or lifted beyond perianth mouth (capsule).

falcate: shaped like a sickle (e.g., leaves of *Herbertus oldfieldianus*, Fig. 11: 2).

fascicle (rhizoids): bundle, bunched together (e.g., *Bazzania monilinervis*, Fig. 102: 8).

fenestrae (singular: **fenestra**): literally windows, clear gaps between a network of opaque thickenings of capsule wall cells; may result from branching and anastomosing of semi-annular bands.

fertile: with archegonia, antheridia or perianths present.

-fid: a suffix denoting a division, e.g., 2-fid: divided in two, 3-fid: divided in three; usually referring to the number of lobes of a leaf or underleaf.

fimbriolate: with a fine fringe of hairs or teeth (diminutive of fimbriate).

first branch underleaf: the first underleaf to form on a terminal branch (cf. first branch leaf); it may be undivided (*Lepidozia acantha*, Fig. 41: 3) or variously lobed (*Lepidozia pumila*, Fig. 42: 2).

flaccid: soft, limp.

flagellae: thin, whip-like ventral-intercalary branches that are microphyllous and geotropic, commonly seen in *Lepidoziaceae*.

flagelliform: of a leafy main shoot or branch that becomes attenuated and bears small and remote leaves distally (microphyllous).

foliose: leafy or leaf-like, e.g., a foliose (rather than spicate) androecium.

foot: base of sporophyte embedded in the gametophyte (e.g., *Trichotemnoma corrugatum*, Fig. 124: 7).

***Frullania*-type branch**: terminal branch replacing the postical half of a lateral leaf, and originating from the ventral half of a lateral merophyte segment; the remaining half-leaf is dorsal (e.g., *Telaranea lindenbergii* var. *papillata*, Fig. 69: 1).

fungal lumps: structures formed by degenerating hyphae unique to *Treubia* and *Haplomitrium* (Fig. 4a–b).

furcate: forked.

fuscous: dark, dull brownish; dusky.

fusiform (oil-bodies, perianths): narrowly elliptical and tapering at both ends, spindle-shaped.

galeate: helmet-shaped.

gametangium: structure bearing gametes (e.g., antheridium, archegonium).

gametophyte: the gamete-producing generation of the liverwort or hornwort, including thallus, or stem and leaves, but also including parts surrounding and protecting the male and female sites of reproduction. Cf. sporophyte.

gemmae (singular: **gemma**): chlorophyllous vegetative propagules produced on the leaf surface or margin and which fall off and establish new plants (e.g., *Jackiella curvata*, Fig. 137: 11). They are usually spherical masses of cells that form as outgrowths from the leaf margin or surface; they also may form in chains.

gemmiferous: gemmae-bearing, as in the gemmiferous filaments of *Diplophyllum gemmiparum.*

gemmiparous: bearing gemmae.

geniculate: bent, like a bent knee.

geotropic (branches): usually in reference to stolons or microphyllous branches that grow downward, acting as roots to anchor the stems (e.g., *Acromastigum verticale*, Fig. 86: 1).

gibbous: bulging or swollen on one side.

glaucescent: having a somewhat glaucous appearance.

glaucous: having a white or grey waxy surface coating (e.g., *Lepidozia digitata*, Plate 5A).

glomeromycote: a member of the division *Glomeromycota* of the fungal kingdom that includes most of the fungi that form obligate symbiotic relationships with vascular plants and bryophytes.

-gonous (perianth): angled, e.g., 3–4-gonous = having three or four angles in cross section.

gutter: a distinct leaf-free zone along the dorsal stem surface created by lateral leaves that do not attain the stem midline.

guttulate: leaf surface with a few large, coarse, high and spherical papillae per cell, the surface then appearing as if speckled with spherical dots of oil or resin (e.g., *Balantiopsis rosea*). Also in reference to the cell lumen being rounded because of strong wall thickening (e.g., *Gymnomitrion*).

gynoecium (plural: **gynoecia**): the site of female reproduction, including protecting scales or leaves and the archegonia (e.g., *Chandonanthus squarrosus*, Fig. 139: 1).

gyre: a single whorl of two lateral leaves and an underleaf.

habitus: the overall appearance of a plant or colony of plants.

half-leaf: foliar structure associated with a terminal branch which replaces the other half of the leaf (e.g., *Telaranea tuberifera*, Fig. 64: 13).

half-underleaf: foliar structure associated with a terminal branch which replaces the other half of the underleaf (e.g., *Lepidozia pumila*, Fig. 42: 3).

hamate: hook-shaped.

haustorial collar: zone of cells at the upper end of the sporophyte foot where it joins the gametophyte; it serves to increase the surface area used to transfer nutrients from the gametophyte to the developing sporophyte.

helophytic: tolerating exposure to full sunlight.

heteroecious: the sexual condition of a species, subspecies or variety involving more than one arrangement of gametangia on the same plant or on differing plants; variable in its sexuality, appearing to be variously monoecious and dioecious.

hispid: covered with short stiff hairs.

Holarctic: relating to the northern parts of the New and Old Worlds, and used somewhat loosely to comprise the temperate, subarctic and arctic regions; especially used to describe a pattern of distribution.

homomallous (leaves): uniformly curving or bending to one side of the stem (e.g., *Herbertus oldfieldianus*, Fig. 11: 8).

horizontal: leaf plane (dorsal view) in which the leaf lies nearly parallel to the dorsal stem surface.

hyaline (cells): used in reference to parts of the leaf or plant lacking chloroplasts (e.g., underleaves of *Bazzania adnexa*, Fig. 94: 10). Hyaline cells appear colorless under the microscope, but whitish when viewed with the eye or with a hand lens. Also used to describe oil-bodies that are colorless.

hyaloderm/hyalodermis: outer layer of cells on the stem (cortex, q.v.) which are larger and thinner-walled than those within (e.g., *Telaranea tetrapila*, Fig. 61: 9). In some taxa the hyaloderm collapses (e.g., *Wettsteinia schusteriana*, Fig. 135: 9).

hygrophyte (hygrophytic): a plant that normally grows under conditions that are always very wet.

hymenophyll: a fern of the family *Hymenophyllaceae*, sometimes called a filmy fern.

hyperpáramo: a narrow zone with scarce vegetation between the grasslands (páramo) and the snow line in the Neotropics at ca. 4000 m.

hyphae: microscopic fungal threads (cf. mycorrhizae).

imbricate (leaves): overlapping loosely. Cf. julaceous.

incised: deeply and narrowly cut into sharp divisions separated by narrow sinuses.

included (perianth): surrounded by gynoecial bracts.

incrassate: with thickened cell walls.

incubous: leaf orientation in which the leaf edge facing the shoot apex is visible from above; also used to describe leaf insertion lines. Cf. succubous and transverse.

incurved (leaf apices and margins): with apices that are curved toward the central axis of the plant (e.g., *Lophozia autoica*, Fig. 140: 2) or margins that are curved inward toward the adaxial center of the leaf. Cf. recurved.

indeterminate: unlimited in growth.

infuscated: tinted with brown pigments.

innovation: a branch originating from directly below the perianth or, typically, associated with a bract or bracteole (e.g., *Diplophyllum dioicum*, Fig. 166: 10).

insertion: the line of leaf attachment on stem; often expressed as the angle the leaf makes to the stem. Cf. incubous, succubous and transverse.

insolated: exposed to full sunlight.

intercalary: positioned between base and apex of stem, used in reference to position of androecium following continuing vegetative growth.

intercalary branching: type of branching in which new branches are delayed in origin, developing from mature sectors of axes (as opposed to branches laid down closely to the apical cell at the stem apex, i.e., terminal branches), and are marked by a basal collar of ruptured stem cortical cells that are pushed up by the branch. There are two types: lateral-intercalary branches and ventral-intercalary branches.

intramarginal (cells): rows of cells interior to the marginal row.

involute (leaf margins): tightly inrolled; rolled upward and inward (adaxially).

isodiametric (cells): equal in width as length, not elongated.

isophyllous (plants): having underleaves that are similar to the lateral leaves in shape and size. The alternative state is anisophyllous (e.g., *Hygrolembidium triquetrum*, Fig. 114: 4).

jacket-cells: the cells that compose the wall of the antheridium body or sperm-containing sac.

julaceous (leaves): smoothly cylindrical and worm-like in appearance; used in reference to leaves overlapping very tightly so as to appear to form a continuous surface so that none of the stem is visible. Cf. imbricate.

keel (leaves, perianths): commissure or line formed by a sharp fold of a leaf, U- or V-shaped in section (e.g., the keel of a complicate-bilobed leaf of *Scapania nemorosa*, Fig. 171: 5); also used for the juncture of two sides of a perianth, e.g., a trigonous perianth is 3-keeled in *Chiloscyphus* spp.

lacinia (plural: **laciniae**): a narrow, tapered division, see laciniate.

laciniate: slashed into narrow, tapering divisions, each coarser than cilia and more than one cell wide at least toward base (e.g., *Lepidozia ulothrix*, Fig. 46: 6).

lamella (plural: **lamellae**): blade of tissue on the leaf or perianth surface that stands erect from the main lamina. Commonly present on the leaves of *Schistochila*; also seen on the perianth surface of *Lamellocolea*.

lamina (plural: **laminae**): a flat structure of a plant, usually either the leaf blade or the thallus; commonly in reference to that part of the leaf basal to the lobes.

lanceolate: narrowly ovate-acuminate and tapered from near the base; lance-shaped.

lateral-intercalary branch: type of branch that originates from the axil of a lateral leaf. A collar of cortical cells surrounds the base of the new branch, and the new branch is usually shorter than the parent branch (e.g., *Triandrophyllum subtrifidum*, Fig. 16: 1). Cf. intercalary branching.

lateral leaves: leaves (of leafy and pseudoleafy liverworts) that are arranged in two rows. They are often asymmetrical and are nearly always larger than underleaves.

lateral merophyte: the cells that give rise to lateral leaves (see under merophyte).

leaf lobe: part of a folded leaf (e.g., *Clandarium xiphophyllum*, Fig. 173: 9) or a divided leaf (e.g., *Lepidozia hirta*, Fig. 44: 3).

***Lejeunea*-type branch**: a type of terminal branch in which the new branch arises behind an unmodified leaf and typically arises from the ventral half of the basiscopic portion of a segment; the branch lacks a distinct basal collar. Widespread in *Lejeuneaceae*.

***Lejeunea*-type innovation**: a terminal-type branch originating directly below a perianth in which the leaf nearest the branching point, and the first leaf to form, is a lateral leaf. Cf. *Pycnolejeunea*-type innovation.

lenticular: lens-shaped, biconvex.

leptodermous: uniformly thin-walled.

ligulate: strap-shaped; moderately long and narrow, with sides parallel.

lingulate: tongue-shaped, widest at or near the base (e.g., leaves of *Jamesoniella kirkii*, Fig. 155: 5).

lobule: a sac-like structure. The lobule is at the basiscopic margin of the leaf (in all *Lejeuneaceae*) or replaces an underleaf lobe (in *Lepidolaena*). Where the lobule is part of a lateral leaf it is formed by a folding of the leaf margin (e.g., in *Radula*), or by a ventral lobe becoming concave or helmet-shaped (e.g., in *Frullania*). Also, the sac-like swelling at the base of male bracts formed by the inflexed or involute basiscopic margin of the bract. In epiphytic plants the lobule function is to retain water.

longitudinal insertion: with an insertion line parallel to the stem axis (e.g., *Telaranea remotifolia*, Fig. 65: 8). Cf. transverse insertion.

longitudinal wall: the longer pair of the four radial walls (q.v.) of a rectangular cell that is part of a cylinder or sphere; the vertical wall.

lumen (plural: **lumina**): the cell cavity bounded by the cell walls.

malleable: varying in form, the variation often caused by differing environmental conditions.

mamillose: with mamillae; having small nipple-like projections.

marsupium (plural: **marsupia**): a sac-like, pendent perigynium derived from stem tissue and acting as a sporophyte protective device (e.g., *Trichotemnoma corrugatum*, Fig. 124: 6, 7).

medulla: internal tissue of the stem, usually of thin-walled cells, and surrounded by the cortex. Hence medullary cells.

merophyte: (1) a single cell formed by the division of a shoot apical cell at one of its faces; (2) a group of cells derived from that single cell; (3) the structures derived from these cells; e.g., in leafy hepatics, from the one-celled merophyte formed at the apex a merophyte consisting of a single leaf and associated stem tissue is ultimately developed.

***Microlepidozia*-type branch**: terminal branch replacing the antical half of a leaf, and originating from the dorsal half of lateral merophyte segment; the remaining half-leaf is ventral (e.g., *Kurzia hippuroides*, Fig. 79: 1).

microphyllous (of a shoot): small leaved; bearing leaves which are minute compared to the normal lateral leaves, e.g., of stolons or flagella (e.g., the microphyllous and geotropic ventral shoot of *Acromastigum verticale*, Fig. 86: 1).

middle lamella: the cementing layer between cellulose walls of adjacent cells; it may be colorless or pigmented and then often quite distinct.

monandrous (male bracts): with only one antheridium.

moniliform: like a string of beads.

monoecious (noun: **monoecy**): with both gynoecia and androecia on the same plant (on the same or different branches, cf. paroecious and autoecious for these distinctions) (e.g., *Lophozia monoica*, Fig. 141: 1). The opposite state is dioecious.

monopodial branching: manner of branching in which there is a leading main stem and smaller primary branches.

monotypic: containing a single element, especially used to refer to a genus comprising a single species.

mucilage: thick clear gelatinous fluid secreted by slime papillae (e.g., in *Haplomitrium*).

mucro: an abrupt short apical tooth on an otherwise obtuse leaf apex.

multistratose: more than one cell layer thick, as seen in cross section through a leaf or thallus (e.g., *Hygrolembidium triquetrum*, Fig. 114: 6).

mycorrhizal: infected with fungal hyphae (mycorrhizae) present in stems or thallus (e.g., *Lophozia drucei*, Fig. 143: 14). These appear as brown threads sometimes in a dense mass, usually within the host cells, but sometimes in spaces between the cells (e.g., *Riccardia intercellula*, cf. Brown and Braggins, 1989, fig. 13: 3).

navicullariform: boat-shaped.

Neotropics: the tropics of the New World, i.e., the American tropics.

nitid: shining, glossy.

nodose (trigones, cell walls): with knot-like swellings.

nodulose (trigones, cell walls): with small knot-like swellings.

oblate: nearly circular, but flattened above and below so that width is greater than length.

obliquely spreading (leaves): with leaf apex at 35–55° to stem.

obpyriform: pear-shaped but with the widest part farthest from the base or point of attachment.

obtrapezoidal (leaf disc shape): quadrilateral with none of the four sides parallel and widest distally.

ocellus (plural: **ocelli**): an unusually large cell having one or more large oil-bodies and lacking chloroplasts; found in leaves, bracts and perianths (e.g., *Frullania* spp., some *Lejeuneaceae*).

oil-bodies: variously shaped coherent collections of oil-droplets found in the cells of most liverworts (but not present in hornworts or mosses) (e.g., *Mnioloma novae-zelandiae*, Fig. 122: 10). They lack the green pigment of chloroplasts but can be the same size. Usually with a granular or papillose texture and about 5–10 μm long, disappearing on drying of specimens.

one-phase development or ontogeny: a pattern seen in the outermost layer of capsule wall cells in which all the longitudinal, radial walls have nodular thickenings (e.g., *Chandonanthus squarrosus*, Fig. 139: 5). Cf. two-phase development.

opaque: not transparent or translucent.

opposite/opposed (arrangement of leaves): of two leaves located exactly opposite on the two sides of a stem rather than staggered. An uncommon condition in the leafy liverworts. Cf. alternate.

Paleotropics: the tropics of the Old World, i.e., the Asian and Pacific tropics.

palmate: with lobes radiating from a central point.

papillae (singular: **papilla**): hemispherical or short elliptic thickenings of the lamina surface.

papillate (spore or leaf surfaces): having papillae.

papillose (surfaces of spore, leaf and perianth): appearing (under light microscope) coarsely roughened by collections of hemispheres or globules, usually ca. (2)4–10(15) per leaf cell and juxtaposed (e.g., *Jamesoniella colorata*, Fig. 157: 7).

paramecioid (oil-body shape): shaped like *Paramecium*, a single-celled animal, basically ellipsoidal but with a slight waist at the middle and wider and more acute-tipped at one end than the other.

paraphyllia (singular: **paraphyllium**): multicellular outgrowths from the stem that may be

hair-like and simple or branched or are leaf-like (e.g., *Chandonanthus squarrosus*, Fig. 138: 1, 2).

paraphyses (singular: **paraphysis**): small, mostly filiform or lanceolate structures intermixed with antheridia.

parenchymatous: composed of undifferentiated cells, usually thin-walled and isodiametric; parenchyma is tissue comprised of such cells.

parenthosome: a curved, banded structure found on either side of a dolipore septum (q.v.) which may be perforate, imperforate or vesiculate (Fig. 3c).

paroecious (noun: **paroecy**): having androecia and gynoecia on the same axis but not mixed, with antheridia in axils of bracts immediately below the bracts surrounding the archegonia (e.g., *Diplophyllum novum*, Fig. 168: 1). A type of monoecy (q.v.).

patent (leaves): spreading at 45° or more to the stem. Cf. appressed and oblique.

paucidentate: with few teeth.

pectinate: of shoots with narrow leaves oriented at ± right angles to the stem, rather like the teeth of a blunt comb.

pellucid: penetrated by light but not transparent.

perianth: a tube of foliar origin in most leafy liverworts. Its function is to protect the developing sporophyte. In shape it can be bulbous, trigonous, flattened or cylindrical, or with a number of folds or keels, and it is either narrowed at the mouth (e.g., *Jamesoniella colorata*, Fig. 157: 8) or not (e.g., *Telaranea herzogii*, Fig. 76: 1) . The surface can be warted, papillose or ciliate. Serves the same function as a coelocaule and perigynium.

perigynium: a rather fleshy, tubular, sporophyte protective device that is derived from axial cells below and peripheral to the archegonial cluster; a reduced perianth is often present at the summit of the perigynium (e.g., *Isotachis*); a perigynium may or may not be associated with a shoot calyptra.

persistent (leaves): long-lasting. The opposite state is caducous.

piceous: glossy black.

piliferous (of leaf apex or perianth mouth): with a long hair point (e.g., *Pseudomarsupidium piliferum*, Fig. 129: 1, 2).

pinnate: with side branches from the main shoot that are shorter than the main shoot and tend to be in regular rows (e.g., *Telaranea tetrapila*, Fig. 61: 10).

pinnulate: having each pinna subdivided.

pit (pitted): minute perforation in walls between adjacent cells.

plagiotropic: growing at an oblique angle or horizontally. Cf. geotropic.

plane: used in reference to a leaf that is flattish, i.e., neither concave nor convex, or a margin neither incurved nor recurved.

plica (plural: **plicae**): a fold.

plicate (usually referring to the perianth): with longitudinal ribs of tissue (plicae, folds), e.g., perianth of *Lophozia drucei* (Fig. 143: 2).

plurilobulate: with several or many lobules.

pluripapillose (lamina surface): having numerous papilla per cell (e.g., *Clandarium xiphophyllum*, Fig. 173: 2, 4).

pluriplicate: with several or many folds.

polyandrous (male bracts): with several to many antheridia.

polymorphous: very variable in form.

polyphyletic: a group of taxa without a single common ancestor, a group of mixed origin.

polystratose (lamina): more than one cell thick, usually appearing thick and succulent to the eye.

postical: facing toward the base of a plant. Usually used to refer to the margin of a (obliquely or longitudinally inserted) leaf that is nearest the shoot base. Cf. antical.

primary branch: any branch arising from the main axis (cf. secondary branch).

prismatic (perianth): triangular in section; sharply trigonous.

processes: used in reference to projecting cells or rows of cells out of the plane of the leaf, usually from the leaf base or leaf lobe sinuses (e.g., *Kurzia hippuroides* var. *ornata*, Fig. 79: 2).

procumbent: lying flat and scarcely or loosely attached to the substrate.

prosenchymatous: tissue that is composed of elongated cells that overlap at their tips.

prostrate: lying flat on the substrate, closely or firmly attached.

proximal: the basal part of a shoot or leaf. Cf. distal.

pruinose: having a white powdery coating.

pseudodichotomous branching: branching in leafy liverworts where the new *Frullania*-type branch is subequal to the main axis in vigor and the main axis loses its dominance; the branches often originate from only one side of the axis. Seen most clearly in *Acromastigum* and *Bazzania* (e.g., *Bazzania hochstetteri*, Fig. 97: 6).

pseudodioecious: state in which plants appear to be dioecious with archegonia and antheridia appearing on separate plants when in fact they belong to the same plant but the connection in the older parts of the stem has decayed.

pseudoparenchyma: a dense tissue formed by hyphae growing closely together where individual hyphal components of the tissue are no longer distinguishable (Fig. 4c).

***Pycnolejeunea*-type innovation**: a terminal-type branch originating directly below a perianth in which the foliar structure nearest the branching point, and the first foliar structure to form, is an underleaf. Cf. *Lejeunea*-type innovation.

pyriform: pear-shaped.

radial wall: one of four walls of a cell that is part of a cylinder or sphere that lies along a line radiating from the center of the cylinder or sphere. (In wood anatomy a radial wall is parallel to a ray.) Cf. tangential wall.

***Radula*-type branch**: a type of terminal branch in which the new branch arises behind an unmodified leaf and typically arises from the ventral half of the merophyte segment; the branch lacks a basal collar and is often connate with the base of the associated stem leaf. Occurring, e.g., in *Radula* and in *Schistochilaceae*.

ramified: branched; a densely ramified plant is densely branched (e.g., *Telaranea tridactylis*, Fig. 53: 3).

receptacle: the closely juxtaposed, large bracts within which the antheridia or archegonia occur in some *Haplomitrium* species.

recurved (of leaf apices or margins): curved downward and backward, i.e., abaxially or away from the central axis of the plant (e.g., leaf lobes of *Diplophyllum verrucosum*, Fig. 164: 2) or the leaf (e.g., leaf margins of *Isophyllaria attenuata*, Fig. 17: 2). Cf. incurved.

reduced: smaller or structurally simpler than in ancestral forms.

regeneration: a form of vegetative regeneration developed from a mature cell that becomes meristematic, forming a minute superficial bud capable of developing into a new shoot; e.g., *Chiloscyphus* spp.

remote (leaves along a stem): widely separated (e.g., *Telaranea remotifolia*, Fig. 65: 8). The term, as used here, does not imply any particular distance between leaves, despite the common meaning in English. The term distant is synonymous.

reniform: kidney-shaped.

repand: having an uneven, slightly sinuous margin.

retuse: having a notch at the apex, indented by a rounded sinus; often in reference to a leaf with a rounded or truncate apex in the center of which is a rounded sinus; cf. emarginated, in which the sinus is acute.

revolute: strongly recurved. Cf. involute.

rhizoids: single-celled hairs, usually colorless or crimson, that anchor the plant to its substrate. They usually have their origin on the stem, and are usually clustered at the underleaf base in leafy liverworts. They may originate from underleaf cells (e.g., in *Telaranea*).

rhizoid initial: a small, thin-walled cell, with the potential to develop into a rhizoid.

rhizome: horizontal underground stem that gives rise to aerial branches.

rostellum: a small beak.

rostrum: beaked (e.g., the perianth summit of *Frullania* spp.).

rotundate: rounded, like the arc of a circle.

rudimentary: incompletely developed, vestigial.

saccate (describing a modified leaf or thallus margin): folded into a bag-shaped structure that encloses a space but is open at one end or on one side.

saxicolous: dwelling on rocks.

scalariform (capsule wall thickenings): ladder-like arrangement of the thickenings.

scalloped (margin): widely crenate.

secondary branch: any branch arising from a primary branch.

secund (leaves): turned or bent toward one side.

semiannular bands (capsule wall cells): U-shaped, band-like thickenings of the inner (and exceptionally the outer) capsule wall cells, occurring on the two radial walls and the outer tangential wall, but absent from the inner tangential wall (e.g., capsule wall of *Isolembidium anomalum*, Fig. 112: 1, 5).

septum (plural: **septa**): used here to refer to the cross walls of a uniseriate (or in part biseriate) lobe, e.g., the leaf lobes of *Telaranea praenitens* are swollen and projecting (Fig. 55: 5). Also used with reference to the swelling and thickening of marginal cells of the disc (e.g., *Lepidozia procera*, Fig. 30: 8).

serrate (lamina margin): toothed, but with the teeth set at an angle.

serrulate (lamina margin): finely serrate.

sessile: without a stalk, sitting close upon the body that supports it; e.g., slime papilla on underleaf margin or describing an archegoniophore.

seta (plural: **setae**): non-chlorophyllose, sporophytic stalk that elevates the capsule away from the leafy or thallose plant; usually extending rapidly by cell elongation when spores are mature.

setiform: bristle-like.

setose: with bristles or stiff hairs; setaceous (bristle-like).

sheet-like thickenings (of capsule wall cells): diffuse thickenings of longitudinal walls of inner and outer layers of capsule wall cells (e.g., *Megalembidium insulanum*, Fig. 118: 9 and Fig. 119: 8). See Schuster (1966b, pp. 592–597) for explanation and illustration of capsule wall thickenings.

shoot: stem and leaves taken together as a structure, or in the case of thallose forms, a branch of a thallus. A single unbranched axis.

shoot calyptra: an often firm and fleshy structure derived from the archegonial venter and axial tissue at the base of and peripheral to the archegonium; unfertilized archegonia are carried up the structure and are present on its sides.

"Shrot-Korn" type (oil-bodies): many minute homogeneous oil-droplets (see p. 47: K).

sigmoidal: S-shaped.

simple (shoot): unbranched.
sinuate: having the margin uneven, with flat edges having alternating concavities and convexities (slightly sinuate is repand, q.v.).
sinuous: applied to flat edges strongly curving in and out; of leaf margins. When used to describe cell walls, it refers to shared cell walls that can vary in thickness but are not lumpy (termed nodulose).
sinus: the gap between two adjacent lobes (e.g., of a leaf or underleaf).
slime papilla: specialized cell that produces mucilage, clavate and rounded at the apex, thin-walled, hyaline and sessile or stalked and found at the terminus of a lobe or tooth of a leaf or underleaf or at thallus tips (e.g., *Telaranea tridactylis*, Fig. 54: 15).
south temperate: of the Southern Hemisphere's temperate zone.
snow tussock: tall tussock-forming grasses of the genus *Chionochloa*.
spatulate: narrow proximally, widening to become broad distally, flat throughout.
spherules (of oil-bodies): tiny spheres.
spicate: literally like ears of grain, forming a spike-like, racemic grass inflorescence; often used to describe the form of an androecium.
spindle-shaped (of oil-bodies): ellipsoidal but with narrowly acute ends (cf. fusiform).
spinose: a surface or margin covered in spines.
spinulose: a surface or margin covered in fine spines.
sporeling: the stage of a bryophyte between spore germination and maturity.
spores: the means of dispersal for liverworts and hornworts; cellular objects produced in the capsule that disperse to give rise to new plants. They are usually spherical and small (less than ca. 30 μm diameter), single-celled (in all liverworts), or few-celled (in some hornworts) and usually have distinctive patterning on their surface (e.g., *Jamesoniella colorata*, Fig. 157: 11).
sporophyte: the diploid, spore-producing generation of the liverwort (consisting of capsule, seta, and foot), which produces haploid spores and elaters. Cf. gametophyte.
spreading (leaves): the angle between leaf and stem; obliquely spreading = leaf apex is at 35–55° to the stem; widely spreading = leaf apex at 60–80°. Cf. suberect, squarrose. The term patent is also used to refer to leaves that are obliquely to broadly spreading from the stem.
squarrose (leaves and underleaves): the angle between leaf and stem is 90° or more.
stellate: star-shaped.
stem: the cylindrical part of a leafy liverwort that supports the leaves and reproductive parts.
stem midline: an imaginary central line along the dorsal surface of the stem. Leaves are said either to attain this midline, cross the midline and are then interlocking, or do not attain the midline in which case a distinct "gutter" (q.v.) on the dorsal surface may be apparent.
stem perigynium: see perigynium.
stenotypic: with an abnormally low level of variation.
stipitate: with a short stalk-like base; of perianths elevated by an apparent stalk (e.g., *Dinckleria pleurata*).
stolon: horizontal stem of the plant that creeps over or beneath the substrate and gives rise to aerial branches (e.g., *Cryptochila grandiflora*, Fig. 162: 1).
striate (surface of leaves, perianths): with linear, ridge-like markings oriented parallel with one another, appearing streaked (e.g., *Tritomaria exsecta*, Fig. 145: 8).
striolate (surface of leaves, perianths): with striolae, i.e., fine linear, ridge-like markings (e.g., *Telaranea patentissima*, Fig. 60: 9).
stylus: a uniseriate or multiseriate, subulate to triangular structure found between the lobule and stem in certain leafy liverworts (e.g., *Frullania*).

subamplexicaul: leaves extending their bases slightly and transversely onto the stem, clasping.
subcanaliculate: weakly channeled.
subcarinate: weakly keeled.
subcucullate: weakly hooded.
subcupulate: shaped somewhat like a small cup.
suberect (leaves): with leaf apex at 15–35° to stem.
subfalcate: weakly sickle-shaped.
subisophyllous (plants): with underleaves similar to the lateral leaves in shape (degree of lobing etc.), but smaller (ca. 60%–90% of the size) (e.g., *Triandrophyllum subtrifidum*, Fig. 16: 1).
subsquarrose: leaves almost at 90° to the stem, at an angle greater than widely spreading.
subulate: with a long, narrow, needle-like point.
subvitta: a weakly differentiated band of larger cells in a leaf.
subvittate (leaf): with a band of cells that each are larger than the rest, but only weakly so (e.g., *Acromastigum marginatum*, Fig. 89: 1).
succubous: leaf orientation in which the leaf edge facing the shoot base is visible from above, like shingles on a roof; also used to describe leaf insertion lines (e.g., *Solenostoma hodgsoniae*, Fig. 153: 1). Cf. incubous and transverse.
sulcate: grooved or furrowed; of leaf lobes or (perianth) the longitudinal grooves or furrows associated with plicae (e.g., leaves and bracts of *Isophyllaria attenuata*, Fig. 18: 1).
sulcus (plural: **sulci**): a groove.
superposed (cells): placed vertically on top of each other.
tangential wall: one of two walls of a cell that is part of a cylinder or sphere that lies in the plane of the circumference of the object. (In wood anatomy the tangential plane is perpendicular to the radial plane.) Cf. radial wall.
taxon: a taxonomic entity at an unspecified rank (e.g., genus, section, species, subspecies, variety).
teeth: projections composed of one to many cells, usually in the plane of the lamina (cf. processes), e.g., *Scapania nemorosa* (Fig. 171: 8).
terete: round in cross section, not flattened.
terminal branch: type of branch originating from merophyte cells cut from the apical cell at the shoot apex, a collar of cells at the branch base is nearly always lacking (e.g., *Bazzania nova*, Fig. 99: 4). Cf. intercalary branching.
terrestrial: dwelling on ground.
terricolous: dwelling on the ground.
tetrad (spores): a group of four.
thallose: of or pertaining to a thallus.
thallus: the dorsiventrally flattened gametophyte not differentiated into stem and leaves, and is often more than one cell thick; primarily in reference to the gametophyte form in *Metzgeriales*, *Marchantiales* and *Anthocerotae*.
thecal: used in reference to a branch having a collar or sheath of tissue, i.e., either a ventral- or lateral-intercalary branch. Cf. athecal.
tinted: colored by secondary pigments that are yellow, brown, red or purple (the primary pigment is chlorophyll).
tortuous: irregularly twisted, e.g., elaters.
transverse insertion: the insertion of the leaf on the stem is at right angles to the stem direction (e.g., *Adelanthus occlusus*, Fig. 134: 3). Cf. longitudinal insertion, incubous and succubous.
trapezoidal: quadrilateral with none of the four sides parallel.

trigone: a thickening at cell wall junctions. Usually three walls meet at the junction, so that the thickening is 3-sided (e.g., *Solenostoma hodgsoniae*, Fig. 153: 10). Trigones may be large, with sides convex and bulging, or medium and straight-sided, or small and concave-sided, or minute.

trigonous: three-angled, triangular in section.

triquetrous: triangular in section but ridged along the angles.

tristichous (leaf arrangement): arranged in three ranks, i.e., underleaves are present, and similar in size to lateral leaves. Cf. distichous.

truncate: abruptly cut off or squared off at the apex.

trunk hyphae: large aseptate hyphae occurring in glomeromycote fungi. Usually at least five times the diameter of arbuscules in the same cells (Fig. 2c).

tuber: a globose or ellipsoidal structure produced on a stoloniform axis (some *Lepidoziaceae*, e.g., *Telaranea tuberifera*, Fig. 64: 2, 10), or on the ventral surface of a thallus; regarded as a means of asexual reproduction.

tuberculate (surfaces of leaves, perianth and spores): ornamentation with one protuberance per cell and positioned centrally over the cell lumen; each more than 1 and less than 1.5× longer than wide, with regularity of base perimeter and consistency of apex form, knob-like, thick-walled at least at the summit, which is obtuse to rounded to truncate (e.g., *Chiloscyphus leucophyllus*).

tumid: inflated, swollen.

turbinate: shaped like a child's top, obconic, narrow at the attached end, wide and rounded at the free end.

two-phase development or ontogeny: a pattern seen in the outermost layer of capsule wall cells in which approximately quadrate primary cells are without thickenings (or with only local and sporadic thickenings); the primary cells each further subdivide longitudinally by secondary walls that develop pigmented nodular thickenings. Thus a repeating pattern of alternating unthickened and thickened walls is created (e.g., *Lepidozia laevifolia*, Fig. 38: 10).

underleaf: the leaf found on the ventral (lower) side of most leafy liverworts and which is usually smaller than the lateral leaves; it is almost always symmetrical.

undulate (margin): applied to edges waved upward and downward.

uniseriate: arranged in a single row, usually referring to the cells making up a cilium (often used in describing the distal sector of a leaf, underleaf or perianth lobe); also of antheridial stalks (e.g., *Diplophyllum verrucosum*, Fig. 164: 11).

unisexual: having either male or female parts but not both, dioecious.

unispiral (elaters): with a single spiraled thickening band.

unistratose (leaf lamina or thallus): one cell thick. Most leafy liverworts have unistratose leaves (e.g., *Telaranea tridactylis*, Fig. 54: 4). Cf. multistratose and polystratose.

urceolate: urn-shaped.

valve: segments of a capsule after dehiscence, usually four per capsule (e.g., *Cuspidatula monodon*, Fig. 159: 3).

venter: the slightly swollen base of an archegonium, containing the egg, the archegonium otherwise with a neck.

ventral: lower aspect of a prostrate shoot. Cf. dorsal.

ventral-intercalary branching: type of branching in which branches originate from the axils of underleaves (e.g., *Bazzania exempta*, Fig. 105: 1). A collar of cortical cells surrounds the base of the new branch (see under intercalary branching). Synonymous with the older, less-used term postical-intercalary branching.

ventral merophyte: the cells that give rise to underleaves; term often used to express width

(in number of cells) between opposing ventral leaf bases, e.g., having a ventral merophyte X cells wide.

ventricose: swollen, especially on one side toward the base; usually used in reference to male bracts.

vermiculate: a surface with worm-like patterning.

vermiform: worm-like.

verrucate: with wart-like outgrowths or swellings.

verrucose: with wart-like outgrowths or swellings.

verruculae: warts.

verruculose: with fine wart-like swellings.

vertical: leaf orientation in which the adaxial leaf face is turned to face the stem, the leaves then are seen ± edge-on in dorsal view. (The term does not relate to assurgency.)

vesicles: inflated hyphae produced within the host plant cells by many arbuscular mycorrhizal fungi; often multinucleate and full of lipids (Fig. 2b).

vestigial: said of a structure (leaves, underleaves, teeth) that is reduced to only a trace or remnant (e.g., *Jamesoniella tasmanica*, Fig. 156: 5).

vinaceous: with the color of red wine, a crimson tinting.

vitta: a strip of enlarged cells, often also with thinner walls, running from the base toward the apex of a leaf, or toward the apices of its lobes; usually in median sector of leaf, but may be lateral in position (e.g., *Bazzania monilinervis*, Fig. 102: 2).

wing: a thin, flat extension of the keel of a perianth (e.g., *Chiloscyphus* spp.) or folded leaf (e.g., *Schistochila*) or female bract.

wiry (shoots): with the texture and appearance of wire, stiff and narrow.

xerophyte (xerophytic): a plant that is able to live in a very dry habitat.

***Zoopsis*-type branch**: terminal branch replacing the whole lateral leaf, i.e., it originates from the entire lateral merophyte.

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INDEX

Names in Roman type are accepted names. Names in *italics* are synonyms or invalid names. **Bold** page numbers are principal references for New Zealand taxa. Names in Roman type without bold page numbers are non–New Zealand taxa. Names of taxa treated or discussed in this volume are listed in this index; taxa mentioned in habitat descriptions but not treated in this volume are listed in the Appendix.

Acolea Dumort., 805
Acolea acinacifolia (Hook.f. & Taylor) Trevis., 742
Acolea atrocapillum (Hook.f. & Taylor) Steph., 791
Acolea concinnatus (Lightf.) Dumort., 805
Acolea cuspidata (Berggr.) Steph., 807
Acolea denticulata (Berggr.) Steph., 797
Acolea magellanica C.Massal. & Steph., 792
Acolea stricta (Berggr.) Steph., 809
Acrobolbaceae E.A.Hodgs., **80**, **83**
Acrobolbus Nees, **80**, **84**, **88**
  Subg. Lethocoleopsis Grolle, **88**
Acrobolbus aequaelobus E.A.Hodgs., 641
Acrochila R.M.Schust., **81**
Acrochila caledonica (Steph.) Inoue, 727
Acrolejeunea (Spruce) Schiffn., **90**
Acrolepidozia R.M.Schust., 270, 276
Acrolophozia R.M.Schust., 82, **785**
Acrolophozia fuegiana R.M.Schust., 786
Acrolophozia pectinata R.M.Schust., **786**
Acrolophozia sulcata Hässel, 786
Acromastigum A.Evans, 74, 76, **390**
Acromastigum anisostomum (Lehm. & Lindenb.) A.Evans, **407**
Acromastigum anisostomum var. *minutum* E.A.Hodgs., 408
Acromastigum brachyphyllum A.Evans, **413**
Acromastigum cavifolium R.M.Schust., **392**
Acromastigum colensoanum (Mitt.) A.Evans, **398**
Acromastigum cunninghamii (Steph.) A.Evans, **402**
Acromastigum exile (Lindenb.) A.Evans, 390
Acromastigum integrifolium (Austin) A.Evans, 390, 395
Acromastigum laetevirens (Sande Lac.) A.Evans, 390
Acromastigum marginatum E.A.Hodgs., **405**
Acromastigum martinii E.A.Hodgs., 397
Acromastigum mooreanum (Steph.) E.A.Hodgs., **409**
Acromastigum rigidum R.M.Schust., 391
Acromastigum verticale (Steph.) E.A.Hodgs., **395**
Acroscyphella N.Kitag. & Grolle, **79**
Adelanthaceae (Jörg.) Grolle, **607**
  Tribe *Adelantheae* Jörg., 607
Adelanthus Endl., 608
Adelanthus Mitt., 86, **615**
  Sect. Adelanthus, **616**
  Sect. Calyptrocolea (R.M.Schust.) Grolle, **616**
  Sect. Lindenbergiani Grolle, 616
  Sect. Pittieri Grolle, 616
Adelanthus areomarginatus R.M.Schust., 616
Adelanthus bisetulus (Steph.) Grolle, 610
Adelanthus capillaris (Berggr.) E.A.Hodgs., 621
Adelanthus carabayensis (Mont.) Grolle, 616
Adelanthus decipiens (Hook.) Mitt., 608
Adelanthus falcatus (Hook.) Mitt., **621**
Adelanthus gemmiparus (R.M.Schust.) E.A.Hodgs., **617**
Adelanthus humilis Steph., 610
Adelanthus integerrimus Grolle, 616
Adelanthus lindenbergianus (Lehm.) Mitt., 616
Adelanthus occlusus (Hook.f. & Taylor) Carrington, **625**
Adelanthus pittieri (Steph.) Grolle, 616
Adelanthus schusterianus (Grolle) E.A.Hodgs., 629
Adelanthus squarrosus Grolle, 616
Adelanthus tenuis (J.J.Engel & Grolle) R.M.Schust., 616
Alicularia occlusa (Hook.f. & Taylor) Gottsche, 625
Allisoniella E.A.Hodgs., 82, **570**
  Sect. Allisoniella, **574**
  Sect. Protomarsupella (R.M.Schust.) R.M.Schust., **572**
Allisoniella nigra (Rodway) R.M.Schust., **574**
Allisoniella nigra fo. *subobtusa* R.M.Schust., 575
Allisoniella nigra subsp. nigra var. acutiloba J.J.Engel, **576**
Allisoniella nigra subsp. novaezelandiae R.M.Schust., **574**
Allisoniella nigra subsp. novaezelandiae fo. novaezelandiae, **575**
Allisoniella nigra subsp. novaezelandiae fo. subobtusa R.M.Schust., **575**
Allisoniella nigra var. nigra, 574
Allisoniella obcordata E.A.Hodgs., 574
Allisoniella recurva R.M.Schust., **576**
Allisoniella scottii (R.M.Schust.) R.M.Schust., **572**
Allisoniella subbipartita (C.Massal.) R.M.Schust. & J.J.Engel, 571
Allisoniella tasmanica R.M.Schust., 571
Alobiella (Spruce) Schiffn., 552
Alobiellopsis R.M.Schust., 552
Alobiellopsis heteromorphus (Lehm.) R.M.Schust., 552
Alobiellopsis pillansii (Sim) R.M.Schust., 552
Amphicephalozia R.M.Schust., 82, 567
Amphicephalozia amplexicaulis R.M.Schust., 567
Amphicephalozia geisslerae Pócs & Váňa, 567
Anastrepta (Lindenb.) Schiffn., 638
Anastrophyllum (Spruce) Steph., 83, **673**
  Subg. Crossocalyx, 673
Anastrophyllum auritum (Lehm.) Steph., 674
Anastrophyllum ciliatum Steph., 674
Anastrophyllum crebrifolium (Hook.f. & Taylor) Steph., 674
Anastrophyllum decurvifolium (Sull.) Steph., 674

INDEX

Anastrophyllum donianum (Hook.) Steph., 673
Anastrophyllum incumbens (Lehm. & Lindenb.) Steph., 674
Anastrophyllum involutifolium (Mont.) Steph., 674
Anastrophyllum leucocephalum (Taylor) Steph., 674
Anastrophyllum minutum (Schreb. *ex* Cranz) R.M.Schust., 674
Anastrophyllum monodon (Hook.f. & Taylor) Steph., 727
Anastrophyllum novazelandiae R.M.Schust., **680**
Anastrophyllum papillosum J.J.Engel & Braggins, **681**
Anastrophyllum piligerum (Nees) Spruce, 674
Anastrophyllum schismoides (Mont.) Steph., **675**
Anastrophyllum schismoides var. crassulum J.J.Engel, **680**
Anastrophyllum schismoides var. schismoides, **679**
Anastrophyllum tasmanicum Rodway, 641
Anastrophyllum tristanianum J.J.Engel, 674
Andrewsianthus R.M.Schust., 83, **685**
Subg. Andrewsianthus, **692**
Subg. Cephalolobus (R.M.Schust.) R.M.Schust., **688**
Subg. Pseudotritomaria R.M.Schust., 686
Andrewsianthus australis J.J.Engel, 686
Andrewsianthus bilobus (Mitt.) Grolle, 686
Andrewsianthus carinatus Grolle, 686
Andrewsianthus confusus (R.M.Schust.) R.M.Schust., **693**
Andrewsianthus cuspidatus R.M.Schust., **688**
Andrewsianthus ferrugineus Grolle, 686
Andrewsianthus hodgsoniae (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, **691**
Andrewsianthus lancistipulus Grolle, 686
Andrewsianthus marionensis (S.W.Arnell) Grolle, 686
Andrewsianthus perigonialis (Hook.f. & Taylor) R.M.Schust., **692**
Andrewsianthus planifolius J.J.Engel, 686
Andrewsianthus puniceus (Nees) R.M.Schust. *ex* Grolle, 686
Andrewsianthus scabrellus (C.Massal.) R.M.Schust. *ex* J.J.Engel, 686
Andrewsianthus sphenoloboides (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, 686
Anomacaulis (R.M.Schust.) R.M.Schust., 639
Anomoclada Spruce, 552
Anomylia R.M.Schust., 77
Anthelia (Dumort.) Dumort., 75, **547**
Anthelia julacea (L.) Dumort., 547
Anthelia juratzkana (Limpr.) Trevis., **547**
Antheliaceae R.M.Schust., **546**
Aphanolejeunea A.Evans, **89**
Aplozia acroclada Berggr., 517
Aplozia lacerata Rodway, 517
Aplozia victoriensis Bibby, 707
Apomarsupella R.M.Schust., 784
Apomarsupella africana (Steph.) R.M.Schust., 784
Arachniopsis Spruce, 270, 350
Subg. *Amphidactylopsis* R.M.Schust., 350
Sect. *Tenuifoliae* R.M.Schust., 350
Arachniopsis herzogii (E.A.Hodgs.) E.A.Hodgs., 350
Arachniopsis monocera R.M.Schust. & Grolle, 350
Archaeochaete R.M.Schust., 72, 141
Archaeochaete grolleana R.M.Schust., 141
Archaeochaete kuehnemannii R.M.Schust., 141
Archaeochaete temnomoides R.M.Schust., 141
Archeophylla R.M.Schust., 72, **165**
Archeophylla paradoxa R.M.Schust., 166
Archeophylla pungens (Herzog) R.M.Schust., 166
Archeophylla schusteri (E.A.Hodgs. & Allison) R.M.Schust., **166**
Archilejeunea (Spruce) Schiffn., **90**
Arctoscyphus Hässel, 639
Austrolejeunea (R.M.Schust.) R.M.Schust., **91**
Austrolophozia R.M.Schust., **80**

Balantiopsaceae Mitt., **90**
Balantiopsis Mitt., **90**
Basichiton Trevis., 173
Bazzania Gray, 70, 74, **415**
Sect. Connatae (Steph.) Fulford, **423**
Sect. Exemptae J.J.Engel, **453**
Sect. Glaucobazzania J.J.Engel, **449**
Sect. Protobazzania J.J.Engel, **418**
Sect. Vittatae (Steph.) Fulford, **442**
Bazzania accreta (Lehm. & Lindenb.) Trevis., **418**
Bazzania adnexa (Lehm. & Lindenb.) Trevis., **423**
Bazzania adnexa var. adnexa, **430**
Bazzania adnexa fo. *aucklandica* (Lindenb. & Gottsche) E.A.Hodgs. *ex* Hamlin, 431
Bazzania adnexa var. aucklandica (Lindenb. & Gottsche) J.J.Engel & Merrill, **431**
Bazzania anisostoma (Lehm. & Lindenb.) Trevis., 407
Bazzania atro-virens (Hook.f. & Taylor) Kuntze, 407
Bazzania chilensis (Steph.) Fulford, 416
Bazzania colensoana (Mitt.) Carrington & Pearson, 398
Bazzania convexa (Thunb.) Trevis., 442
Bazzania cunninghamii Steph., 402
Bazzania elegans (Colenso) W.Martin & E.A.Hodgs., 418
Bazzania exempta J.J.Engel, **453**
Bazzania fissistipa (Steph.) Pearson, 442
Bazzania hochstetteri (Reicht.) E.A.Hodgs., **431**
Bazzania involuta (Mont.) Trevis., **418**
Bazzania involuta fo. *elegans* (Colenso) Rodway, 418
Bazzania involuta var. involuta, **421**
Bazzania involuta fo. *submutica* (Lindenb. & Gottsche) E.A.Hodgs. *ex* Hamlin, 422
Bazzania involuta var. submutica (Lindenb. & Gottsche) J.J.Engel & Merrill, **422**
Bazzania lacerata Steph., 425
Bazzania mitteniana (Steph.) Steph., 431
Bazzania monilinervis (Lehm. & Lindenb.) Trevis., **446**
Bazzania mooreana Steph., 409
Bazzania nitida (F.Weber) Grolle, **442**
Bazzania nova J.J.Engel & Merrill, **439**
Bazzania novae-hollandiae (Nees) Carrington & Pearson, 423

INDEX

Bazzania novae-zelandiae (Mitt.) Besch. & C.Massal., **436**
Bazzania nutans (Hook.f. & Taylor) Trevis., 508
Bazzania okaritana Meagher & Glenny, **434**
Bazzania peruviana (Nees) Trevis., 416
Bazzania quadrata (Colenso) W.Martin & E.A.Hodgs., 431
Bazzania reflexistipula (Lindenb. & Gottsche) W.Martin & E.A.Hodgs., 418
Bazzania semicordata (Lindenb. & Gottsche) Kuntze, 423
Bazzania skottsbergii (Steph.) Fulford, 416
Bazzania tayloriana (Mitt.) Kuntze, **449**
Bazzania trilobata (L.) Gray, 416
Bazzania verticalis Steph., 395
Bazzaniaceae Nakai, 194
Blepharidophyllaceae (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, **773**
Blepharidophyllum Ångstr., 88, **779**
Subg. *Clandarium* Grolle, 774
Blepharidophyllum densifolium (Hook.) Ångstr. *ex* C.Massal., 780
Blepharidophyllum vertebrale (Taylor *ex* Gottsche, Lindenb. & Nees) Ångstr., **780**
Blepharidophyllum xiphophyllum Grolle, 775
Blepharostoma (Dumort.) Dumort., 141
Blepharostoma corrugatum Steph., 543
Blepharostoma palmatum Lindb. *ex* Pearson, 161
Blepharostoma pulchellum (Hook.) Steph., 151
Blepharostoma quadrifidum (Mitt.) Pearson, 156
Blepharostoma quadripartitum (Hook.) Trevis., 158
Blepharostoma trichophyllum (L.) Dumort., 141
Blepharostomataceae Müll.Frib., 140
Subfam. *Trichotemnomoideae* R.M.Schust., 542
Bonneria Fulford & J.Taylor, 463
Bonneria furcifolia (Steph.) R.M.Schust., 468
Bragginsella R.M.Schust., **85**, 640
Brevianthus J.J.Engel & R.M.Schust., **85**

Calobryales Campb., **59**
Calobryum Nees, 60
Calobryum gibbsiae Steph., 63
Calypogeia Raddi, 73, **533**
Subg. *Caracoma* Bisch., 534
Subg. *Mnioloma* (Herzog) Bisch., 537
Calypogeia arguta Nees & Mont., 534
Calypogeia bidentula (F.Weber) Nees, 534
Calypogeia fissa (L.) Raddi, 534
Calypogeia longifolia Steph., 534
Calypogeia microstipula (Steph.) Steph., 534
Calypogeia sphagnicola (Arnell & J.Perss.) Warnst. & Loeske, **534**
Calypogeia trichomanis var. *sphagnicola* (Arnell & J.Perss.) Meyl., 534
Calypogeiaceae Arnell, **532**
Calyptrocolea R.M.Schust., 615
Calyptrocolea falcata (Hook.) R.M.Schust., 621
Calyptrocolea gemmipara R.M.Schust., 617
Calyptrocolea occlusa (Hook.f. & Taylor) R.M.Schust., 625
Castanoclobos J.J.Engel & Glenny, **168**
Castanoclobos julaceus (Hatcher *ex* J.J.Engel) J.J.Engel & Glenny, 72, **170**
Cephalojonesia Grolle & Vanden Berghen, 567
Cephalolobus R.M.Schust., 685
Cephalolobus hodgsoniae R.M.Schust., 691
Cephalomitrion R.M.Schust., 83, **568**
Cephalomitrion aterrimum (Steph.) R.M.Schust., **569**
Cephalozia (Dumort.) Dumort., 85, **559**
Subg. Cephalozia, **565**
Subg. *Cephaloziella* Spruce, 578
Subg. Eocephalozia R.M.Schust. *ex* J.J.Engel, **561**
Subg. *Prionolobus* Spruce, 578
Cephalozia africana Váňa, 560
Cephalozia argentea (Hook.f. & Taylor) Lindb., 489
Cephalozia aterrima Steph., 569
Cephalozia austrigena R.M.Schust. *ex* J.J.Engel, **565**
Cephalozia badia (Gottsche) Steph., **561**
Cephalozia badia fo. *minor* Grolle, 561
Cephalozia bicuspidata (L.) Dumort., 560
Cephalozia bicuspidata subsp. *austrigena* R.M.Schust., 565
Cephalozia byssacea (Roth) Dumort., 587
Cephalozia ceratophylla Spruce, 484
Cephalozia chilensis (J.J.Engel & R.M.Schust.) R.M.Schust., 560
Cephalozia ciliolata R.M.Schust., 565
Cephalozia cucullifolia Steph., 561
Cephalozia divaricata (Sm.) Dumort., 588
Cephalozia divaricata var. *verrucosa* C.E.O.Jensen, 600
Cephalozia exiliflora (Taylor *ex* Gottsche, Lindenb. & Nees) Trevis., 595
Cephalozia fissa Steph., 560
Cephalozia fissifolia Steph., 484
Cephalozia furcifolia Steph., 468
Cephalozia heteroica Cooke, 560
Cephalozia heteroica R.M.Schust. & J.J.Engel, 560
Cephalozia kirkii Steph., 471
Cephalozia leitgebiana Carrington & Pearson, 481
Cephalozia macrostipa Steph., 471
Cephalozia multicuspidata (Hook.f. & Taylor) Steph., 657
Cephalozia nutans (Hook.f. & Taylor) Spruce, 508
Cephalozia pachygyna R.M.Schust. *ex* J.J.Engel, **563**
Cephalozia patagonica Fulford, 560
Cephalozia pleniceps (Austin) Lindb., 560
Cephalozia schusteriana J.J.Engel, **563**
Cephalozia setulosa (Leitg.) Spruce, 494
Cephalozia varians (Gottsche) Steph., 600
Cephalozia verrucosa (C.E.O.Jensen) Bryhn & Kaal., 600
Cephaloziaceae Mig., **83**, **551**
Subfam. Alobielloideae R.M.Schust., 552
Subfam. Cephalozioideae, **552**
Subfam. Hygrobielloideae R.M.Schust., 552
Subfam. *Jackielloideae* R.M.Schust., 633

Cephaloziaceae Mig. (*continued*)
Subfam. Odontoschismatoideae Buch *ex* Grolle, 552
Subfam. Schiffnerioideae R.M.Schust., 552
Subfam. Trabacelluloideae (Fulford) R.M.Schust., 552
Cephaloziella (Spruce) Schiffn., 82, 83, **578**
Subg. Cephaloziella, **586**
Subg. Distichopsis R.M.Schust., **605**
Subg. Evansia Müll.Frib., **604**
Subg. Schizophyllum Müll.Frib., **584**
Sect. *Schizophyllum* (Müll.Frib.) Jörg., 584
Cephaloziella aenigmata R.M.Schust., **586**
Cephaloziella alpina Douin, 601
Cephaloziella antarctica Douin, 601
Cephaloziella arctica Bryhn & Douin, 601
Cephaloziella arctica subsp. *subantarctica* R.M.Schust., 602
Cephaloziella aterrima (Steph.) E.A.Hodgs., 569
Cephaloziella aterrima var. *crassigyna* R.M.Schust., 597
Cephaloziella byssacea (Roth) Warnst., **587**
Cephaloziella byssacea subsp. *grandiretis* R.M.Schust., 593
Cephaloziella crassigyna (R.M.Schust.) R.M.Schust., **597**
Cephaloziella densifolia R.M.Schust., **599**
Cephaloziella densifolia var. densifolia, **599**
Cephaloziella densifolia var. dubia R.M.Schust., **599**
Cephaloziella dentata (Raddi) Müll.Frib., 604
Cephaloziella divaricata (Sm.) Schiffn., 588
Cephaloziella dusenii Steph., 579
Cephalozia elachista (Jack.) Schiffn., 584
Cephaloziella exigua R.M.Schust., **603**
Cephaloziella exiliflora (Taylor) Douin, **595**
Cephaloziella gemmata J.J.Engel, 579
Cephaloziella glacialis Douin, 601
Cephaloziella grandiretis (R.M.Schust.) R.M.Schust., **593**
Cephaloziella hispidissima R.M.Schust., **589**
Cephaloziella invisa R.M.Schust., **591**
Cephaloziella muelleriana R.M.Schust., **590**
Cephaloziella nigra (Rodway) Grolle, 574
Cephaloziella nothogena R.M.Schust., **594**
Cephaloziella pellucida R.M.Schust., **605**
Cephaloziella pseudocrassigyna R.M.Schust. *ex* J.J.Engel, **600**
Cephaloziella pulcherrima R.M.Schust., **584**
Cephaloziella pulcherrima subsp. pulcherrima, **585**
Cephaloziella pulcherrima subsp. sphagnicola R.M.Schust., **586**
Cephaloziella rufobrunnea R.M.Schust., **607**
Cephaloziella starkei (Funck *ex* Nees) Schiffn., 588
Cephaloziella subspinosa R.M.Schust., **604**
Cephaloziella varians (Gottsche) Steph., **600**
Cephaloziella varians fo. *minor* Grolle, 601
Cephaloziella varians subsp. subantarctica (R.M.Schust.) R.M.Schust. *ex* J.J.Engel, **602**
Cephaloziella verrucosa (C.E.O.Jensen) Bryhn & Kaal., 600
Cephaloziella verrucosa Steph., 579
Cephaloziellaceae Douin, **83**, **566**
Cephaloziopsis (Spruce) Schiffn., 567
Cesia atrocapilla (Hook.f. & Taylor) Mitt., 791
Cesia cuspidata Berggr., 807
Cesia erosa Carrington & Pearson, 797
Cesia stricta Berggr., 809
Cesia stygia var. *denticulata* Berggr., 797
Cesius Gray, 805
Cesius concinnatus (Lightf.) Gray, 805
Cesiusa Kuntze, 805
Cesiusa acinacifolia (Hook.f. & Taylor) Kuntze, 742
Cesiusa concinnata (Lightf.) Kuntze, 805
Cesiusa atrocapilla (Hook.f. & Taylor) Kuntze, 791
Chaetocolea Spruce, 141
Chaetocoleaceae Fulford, 140
Chaetophyllopsis R.M.Schust., **73**
Chandonanthus Mitt., 84, **640**
Chandonanthus squarrosus (Hook.) Mitt. *ex* Schiffn., **641**
Cheilolejeunea (Spruce) Schiffn., **92**
Chiloscyphus Corda, **77**, **78**
Chloranthelia R.M.Schust., 70, 71, 75, 79, **523**
Chloranthelia berggrenii (Herzog) R.M.Schust., **524**
Chloranthelia denticulata (Steph.) R.M.Schust., 523
Chloranthelia filosa (E.A.Hodgs.) R.M.Schust., 524
Chondrophyllum Herzog, 788
Chondrophyllum cucullatum Herzog, 794
Cincinnulus Dumort., 533
Cincinnulus trichomanis var. *sphagnicolus* (Arnell & J.Perss.) Meyl., 534
Cladopodiella Buch, 552
Clandarium (Grolle) R.M.Schust., 88, **774**
Clandarium clandestinum (Mont.) R.M.Schust., 775
Clandarium gottscheanum (Grolle) R.M.Schust., 774
Clandarium xiphophyllum (Grolle) R.M.Schust., **775**
Clasmatocolea Spruce, **78**, **81**
Cololejeunea (Spruce) Schiffn., **89**
Colura (Dumort.) Dumort., **93**
Cryptochila R.M.Schust., 87, **732**
Subg. Acinaria Grolle, **733**
Subg. Cryptochila, **733**
Subg. Nigritula Grolle, **733**
Sect. Acinaria, **733**
Sect. Spegazzinia Grolle, 733
Cryptochila acinacifolia (Hook.f. & Taylor) Grolle, **742**
Cryptochila grandiflora (Lindenb. & Gottsche) Grolle, **736**
Cryptochila nigrescens (Steph.) Grolle, **734**
Cryptochila paludosa (Steph.) Grolle, 733
Cryptochila pseudocclusa (E.A.Hodgs.) R.M.Schust., **740**
Cryptochila spegazziniana (Spruce) Grolle, 733
Cryptocolea R.M.Schust., 639
Cryptocoleopsis Amakawa, 639
Cryptostipula R.M.Schust., 639
Cuspidatula Steph., 86, **726**
Cuspidatula caledonica Steph., 727

Cuspidatula contracta (Reinw., Blume & Nees) Steph., 727
Cuspidatula monodon (Hook.f. & Taylor) Steph., **727**
Cylindrocolea R.M.Schust., 567
Cylindrocolea atroviridis (Sim.) Váňa, 567
Cylindrocolea novae-caledoniae (Grolle) R.M.Schust., 567
Cylindrocolea tagawae (N.Kitag.) R.M.Schust., 567

Delavayella Steph., 745
Delavayellaceae R.M.Schust., 745
Dendrobazzania R.M.Schust. & W.B.Schofield, 195
Dendrolembidium Herzog, 358, 379
Dendrolembidium insulanum (W.Martin & E.A.Hodgs.) Allison & E.A.Hodgs., 529
Dendrolembidium martinii Herzog, 529
Dendrolembidium tenax (Grev.) Herzog, 379
Dendromastigophora R.M.Schust., **73**
Denotarisia Grolle, 639
Dianthelia R.M.Schust., 805
Dianthelia steerei R.M.Schust., 805
Dichiton Mont., 578
Dinckleria Trev., **85**
Diplasiolejeunea (Spruce) Schiffn., **93**
Diplocolea Amakawa, 639
Diplophyllaceae Potemkin, 746
Diplophyllum (Dumort.) Dumort., 88, 89, **746**
  Subg. Austrodiplophyllum R.M.Schust., **747**
  Subg. Diplophyllum, **747**
  Subg. Macrodiplophyllum Buch, 747
  Subg. *Protodiplophyllum* R.M.Schust., 747
Diplophyllum acutilobum Steph., 747
Diplophyllum africanum S.W.Arnell, 747
Diplophyllum albicans (L.) Dumort., 747
Diplophyllum androgynum J.J.Engel & Merrill, 747
Diplophyllum angustifolium J.J.Engel & Merrill, 747
Diplophyllum densifolium fo. *decurvum* Rodway, 775
Diplophyllum dioicum R.M.Schust., **754**
Diplophyllum domesticum (Gottsche) Steph., **757**
Diplophyllum domesticum var. domesticum, **761**
Diplophyllum domesticum var. icari J.J.Engel & Merrill, **761**
Diplophyllum exsectum (Schmid. *ex* Schrad.) Thériot & Monguillon, 669
Diplophyllum gemmiparum J.J.Engel & Merrill, **751**
Diplophyllum incrassatum J.J.Engel & Merrill, 747
Diplophyllum marionense S.W.Arnell, 747
Diplophyllum novum J.J.Engel & Merrill, **762**
Diplophyllum obtusifolium (Hook.) Dumort., 747
Diplophyllum recurvifolium C.Massal., 747
Diplophyllum squarrosum Steph., 747
Diplophyllum verrucosum R.M.Schust., **748**
Diplophyllum vertebrale (Taylor *ex* Gottsche, Lindenb. & Nees) Steph., 780
Douinia Buch, 746
Drepanolejeunea (Spruce) Schiffn., **93**
Drucella E.A.Hodgs., 70, **385**
Drucella integristipula (Steph.) E.A.Hodgs., **389**

Echinolejeunea R.M.Schust., **93**
Eocalypogeia (R.M.Schust.) R.M.Schust., 533
Eocalypogeia quelpartensis (S.Hatt. & Inoue) R.M.Schust., 533
Eocalypogeia schusterana (S.Hatt. & Mizut.) R.M.Schust., 533
Eoisotachis R.M.Schust., **72**, **75**
Eotrichocolea R.M.Schust., 73, **191**
Eotrichocolea polyacantha (Hook.f. & Taylor) R.M.Schust., **193**
Eremonotus confusus R.M.Schust., 693
Eremonotus Lindb. & Kaal. *ex* Pearson, 639
Evansia Douin & Schiffn., 578, 604
Evansianthus R.M.Schust. & Inoue, 78, 79

Frullania Raddi, **91**
Frullaniaceae Raddi, **90**
Fulfordiella Hässel, 141
Fulfordiella fuegiana Hässel, 142
Fuscocephaloziopsis Fulford, 552

Gackstroemia Trevis., **91**
Geocalycaceae Limpr., **77**
Geocalyx Nees, **84**
Gerhildiella Grolle, 638
Goebeliella Steph., **90**
Goebeliellaceae Verd., **90**
Goebelobryum Grolle, **80**, **88**
Gottschelia Grolle, 639
Grollea R.M.Schust., 75, 107
Grollea antheliopsis R.M.Schust., 107
Grolleaceae (Solari) R.M.Schust., 107
Gymnocolea (Dumort.) Dumort., 638
Gymnocoleopsis (R.M.Schust.) R.M.Schust., 638
Gymnocoleopsis capensis (S.W.Arnell) R.M.Schust., 638
Gymnocoleopsis cylindriformis (Mitt.) R.M.Schust., 638
Gymnocoleopsis multiflorus (Steph.) R.M.Schust., 638
Gymnomitriaceae H.Klinggr., **783**
Gymnomitrion Corda, 83, **805**
Gymnomitrion concinnatum (Lightf.) Corda, 806
Gymnomitrion corallioides Nees, 806
Gymnomitrion cuspidatum (Berggr.) R.M.Schust., **807**
Gymnomitrion incompletum (Gottsche) R.M.Schust., 806
Gymnomitrion laceratum (Steph.) Horik., 806
Gymnomitrion orbiculatum Colenso, 703
Gymnomitrion strictum (Berggr.) R.M.Schust., **809**
Gymnomitrion strictum var. inaequalis R.M.Schust., **811**
Gymnomitrion strictum var. strictum, **810**
Gymnomitrium acinacifolium (Hook.f. & Taylor) Gottsche, 742
Gymnomitrium atrocapillum Hook.f. & Taylor, 791
Gymnomitrium denticulatum (Berggr.) Müll.Frib., 797
Gymnomitrium erosa (Carrington & Pearson) Bastow, 797

Gymnomitrium marionense S.W.Arnell, 791
Gymnomitrium orbiculata Colenso, 703
Gymnomitrium vermiculare Schiffn., 794

Haesselia Grolle & Gradst., 552
Haplomitriaceae Dedecek, **60**
Haplomitrium Nees, **60**
Haplomitrium andinum (Spruce) R.M.Schust., 60
Haplomitrium blumii (Nees) R.M.Schust., 60
Haplomitrium chilensis R.M.Schust., 60
Haplomitrium dentatum (D.Kumar & Udar) J.J.Engel, 60
Haplomitrium gibbsiae (Steph.) R.M.Schust., **63**
Haplomitrium giganteum (Steph.) Grolle, 60
Haplomitrium grollei D.Kumar & Udar, 60
Haplomitrium hookeri (Sm.) Nees, 60
Haplomitrium hookeri var. *minutum* (E.O.Campb.) Barthol.-Began, 65
Haplomitrium indicum (Udar & Chandra) R.M.Schust., 60
Haplomitrium intermedium Berrie, 60
Haplomitrium kashyapii Udar & D.Kumar, 60
Haplomitrium minutum (E.O.Campb.) J.J.Engel & R.M.Schust., **65**
Haplomitrium mnioides (Lindb.) R.M.Schust., 60
Haplomitrium monoicum J.J.Engel, 60
Haplomitrium ovalifolium R.M.Schust., **61**
Harpalejeunea (Spruce) Schiffn., **92**
Hattoria R.M.Schust., 638
Hepatostolonophora J.J.Engel & R.M.Schust., **79**
Herberta alpina (Steph.) E.A.Hodgs., 109
Herbertaceae Müll.Frib., **107**
Herbertia attenuata (Mitt.) Kuntze, 95
Herbertia scolopendra (Hook.) Kuntze, 99
Herbertia spinosissima (Hook.f. & Taylor) Trevis., 201
Herbertus Gray, 74, **108**
Herbertus aduncus (Dicks.) Gray, 109
Herbertus oldfieldianus (Steph.) Rodway, **109**
Herbertus runcinatus (Taylor) Kuntze, 109
Herpetium sect. *Lepidozia* Nees, 195
Herpetium involutum Mont., 418
Herpocladium Mitt., 108
Herzogianthus R.M.Schust., **73**
Herzogiaria Fulford, 71, 107, 141
Herzogiaria teres (Steph.) Fulford, 141
Herzogiariaceae Fulford, 140
Herzogobryum Grolle, 83, **788**
Herzogobryum aterrimum (Steph.) Grolle, 569
Herzogobryum atrocapillum (Hook.f. & Taylor) Grolle, **791**
Herzogobryum cucullatum (Herzog) Grolle, 794
Herzogobryum erosum (Carrington & Pearson) Grolle, 797
Herzogobryum filarium Grolle, 569
Herzogobryum filiforme R.M.Schust., **790**
Herzogobryum molle Grolle, 789
Herzogobryum teres (Carrington & Pearson) Grolle, **792**
Herzogobryum vermiculare (Schiffn.) Grolle, **794**
Heteroscyphus Schiffn., **78**
Horikawaella S.Hatt. & Amakawa, 639
Hyalolepidozia S.W.Arnell *ex* Grolle, 70, 74, 76, **472**
Hyalolepidozia bicuspidata (C.Massal.) S.W.Arnell *ex* Grolle, 473
Hyalolepidozia longiscypha (Taylor) Grolle, 473
Hyalolepidozia microphylla R.M.Schust. *ex* J.J.Engel, **473**
Hyalolepidoziaceae Fulford, 194
Hygrobiella Spruce, 552
Hygrobiella acuminata Herzog, 553
Hygrobiella australis Steph., 521
Hygrolembidium R.M.Schust., 76, 79, **509**
Subg. Hygrolembidium, **517**
Subg. Hygrobiellopsis R.M.Schust., 76, **511**
Hygrolembidium acrocladum (Berggr.) R.M.Schust., **517**
Hygrolembidium andinum (Herzog) R.M.Schust., 510
Hygrolembidium australe (Steph.) Grolle, **521**
Hygrolembidium boschianum (Sande Lac.) R.M.Schust., 510
Hygrolembidium isodictyon (Herzog) R.M.Schust., 517
Hygrolembidium isophyllum R.M.Schust., 510
Hygrolembidium rigidum R.M.Schust. & J.J.Engel, **511**
Hygrolembidium stereophyllum (Herzog) R.M.Schust., 521
Hygrolembidium triquetrum J.J.Engel & R.M.Schust., **513**
Hygrolembidium ventrosum (Mitt.) R.M.Schust., 510

Invisocaulis R.M.Schust., 76, 639
Isolembidium R.M.Schust., 76, **499**
Isolembidium anomalum (Rodway) Grolle, **500**
Isolembidium anomalum var. anomalum, **502**
Isolembidium anomalum var. cucullatum (E.A.Hodgs.) J.J.Engel & R.M.Schust., **503**
Isolembidium cucullatum (E.A.Hodgs.) R.M.Schust., 503
Isopaches Buch, 645
Isopaches bicrenatus (Schmid.) Buch, 665
Isophyllaria E.A.Hodgs. & Allison, 75, **141**
Isophyllaria attenuata (Rodway) E.A.Hodgs., **143**
Isophyllaria fuegiana (Hässel) R.M.Schust., 142
Isophyllaria murrayana E.A.Hodgs. & Allison, 143
Isotachis Mitt., **72**, **74**
Isotachis attenuatus Rodway, 143
Isotachis palmatiloba E.A.Hodgs., 156
Isotachis subtrifida (Hook.f. & Taylor) Mitt., 120
Isotachis triloba Steph., 137
Iwatsukia N.Kitag., 552

Jackiella Schiffn., 80, 86, **634**
Jackiella curvata Allison & E.A.Hodgs., **635**
Jackiella javanica Schiffn., 634
Jackiella sinensis (W.E.Nicholson) Grolle, 634
Jackiellaceae R.M.Schust., **80**, **633**
Jamesoniella (Spruce) Carrington, 87, **713**
Sect. Coloratae Grolle, **714**
Sect. Jamesoniella, **714**

Sect. *Purpurascentes* R.M.Schust., 714
Sect. Robustae Grolle, **714**
Jamesoniella acinacifolia (Hook.f. & Taylor) Berggr., 742
Jamesoniella allisonii E.A.Hodgs., 717
Jamesoniella cambewarrana Steph., 719
Jamesoniella colorata (Lehm.) Schiffn., **722**
Jamesoniella fragilis Steph., 703
Jamesoniella grandiflora (Lindenb. & Gottsche) Jack & Steph., 736
Jamesoniella hectorii Berggr., 736
Jamesoniella inflexo-limbata Herzog, 792
Jamesoniella kirkii Steph., **717**
Jamesoniella monodon (Hook.f. & Taylor) N.Kitag., 727
Jamesoniella nervosa Berggr., 736
Jamesoniella nigrescens Steph., 734
Jamesoniella occlusa (Hook.f. & Taylor) Steph., 625
Jamesoniella patula Steph., 734
Jamesoniella pseudocclusa E.A.Hodgs., 740
Jamesoniella purpurascens Steph., 714
Jamesoniella scolopendrina Berggr., 717
Jamesoniella sonderi (Gottsche) Steph., 736
Jamesoniella tasmanica (Hook.f. & Taylor) Steph., **719**
Jamesoniella teres (Carrington & Pearson) Steph., 792
Jamesoniellaceae, 637
Jubulopsaceae R.M.Schust., **90**
Jubulopsis R.M.Schust., **91**
Jungermannia L., 639
Subg. *Anastrophyllum* Spruce, 673
Subg. *Jamesoniella* Spruce, 713
Sect. *Anthelia* Dumort., 547
Sect. *Cephalozia* Dumort., 559
Sect. *Diplophyllum* Dumort., 746
Sect. *Lophozia* Dumort., 645
Jungermannia acinacifolia Hook.f. & Taylor, 742
Jungermannia acroclada (Berggr.) Steph., 517
Jungermannia adnexa Lehm. & Lindenb., 423
Jungermannia adunca Dicks., 109
Jungermannia albicans L., 747
Jungermannia albula Hook.f. & Taylor, 256
Jungermannia anisostoma Lehm. & Lindenb., 407
Jungermannia argentea Hook.f. & Taylor, 489
Jungermannia atrocapilla (Hook.f. & Taylor) Taylor & Hook.f., 791
Jungermannia atro-virens Hook.f. & Taylor, 407
Jungermannia badia Gottsche, 561
Jungermannia bicrenata Schmid. *ex* Hoffm., 665
Jungermannia bicuspidata L., 560
Jungermannia byssacea Roth, 587
Jungermannia cambewarrana Steph., 703
Jungermannia concinnata Lightf., 806
Jungermannia colorata Lehm., 722
Jungermannia confervoides Raddi, 588
Jungermannia consimilis Colenso, 727
Jungermannia convexa Thunb., 442
Jungermannia densifolia Hook., 780
Jungermannia dispar Mont. *ex* Taylor & Hook.f., 371
Jungermannia divaricata Sm., 588
Jungermannia divaricata var. *exiliflora* Taylor *ex* Gottsche, Lindenb. & Nees, 595
Jungermannia domestica Gottsche, 761
Jungermannia doniana Hook., 673
Jungermannia emarginata Ehrh., 799
Jungermannia excisa Dicks., 662
Jungermannia exiliflora (Taylor *ex* Gottsche, Lindenb. & Nees) Taylor, 595
Jungermannia exsecta Schmid. *ex* Schrad., 667
Jungermannia falcata Hook., 621
Jungermannia fragilis Gottsche, 703
Jungermannia geminiflora Colenso, 727
Jungermannia glaucophylla Hook.f. & Taylor, 259
Jungermannia grandiflora Lindenb. & Gottsche, 736
Jungermannia grandifolia (Berggr.) E.A.Hodgs., 699
Jungermannia hippuroides Hook.f. & Taylor, 371
Jungermannia hodgsoniae Grolle, 699
Jungermannia hookeri Sm., 60
Jungermannia humilissima Colenso, 707
Jungermannia inundata Hook.f. & Taylor, 707
Jungermannia involuta (Mont.) Hook.f. & Taylor, 418
Jungermannia julacea L., 547
Jungermannia juratzkana Limpr., 547
Jungermannia laevifolia Hook.f. & Taylor, 227
Jungermannia lanata Hook., 176
Jungermannia microphylla Hook., 204
Jungermannia mollissima Hook.f. & Taylor, 183
Jungermannia monilinervis Lehm. & Lindenb., 446
Jungermannia monodon Hook.f. & Taylor, 727
Jungermannia multicuspidata Hook.f. & Taylor, 657
Jungermannia nemorosa L., 771
Jungermannia nitida F.Weber, 442
Jungermannia nivalis Sw., 547
Jungermannia novae-hollandiae Nees, 423
Jungermannia nutans Hook.f. & Taylor, 508
Jungermannia occlusa Hook.f. & Taylor, 625
Jungermannia orbiculata (Colenso) Grolle, 703
Jungermannia ovato-trigona (Steph.) Grolle, 697
Jungermannia patentissima Hook.f. & Taylor, 295
Jungermannia paucifolia Colenso, 707
Jungermannia pendulina Hook., 206
Jungermannia perigonialis Hook.f. & Taylor, 692
Jungermannia polyacantha Hook.f. & Taylor, 193
Jungermannia polycarpa Colenso, 707
Jungermannia praenitens Lehm. & Lindenb., 285
Jungermannia propagulifera Gottsche, 662
Jungermannia pulchella Hook., 151
Jungermannia pumila With., 697
Jungermannia punicea Nees, 686
Jungermannia pusilla (Mont.) Hook.f. & Taylor, 621
Jungermannia quadrifida Mitt., 156
Jungermannia quadripartita Hook., 158
Jungermannia reptans L., 196
Jungermannia rufiflora Colenso, 709
Jungermannia schismoides Mont., 675
Jungermannia scolopendra Hook., 99

Jungermannia sonderi Gottsche, 736
Jungermannia squarrosa Hook., 641
Jungermannia starkei Funck *ex* Nees, 588
Jungermannia subtrifida Hook.f. & Taylor, 120
Jungermannia tasmanica Hook.f. & Taylor, 719
Jungermannia tenax Grev., 379
Jungermannia teres Carrington & Pearson, 792
Jungermannia tersa Nees, 695
Jungermannia tetradactyla Hook.f. & Taylor, 336
Jungermannia tomentella Ehrh., 180
Jungermannia tomentosa Sw., 175
Jungermannia totipapillosa E.A.Hodgs., 711
Jungermannia tridactylis Lehm. & Lindenb., 281
Jungermannia trilobata L., 416
Jungermannia ulothrix Schwägr., 256
Jungermannia undulata L., 768
Jungermannia varians Gottsche, 600
Jungermannia ventricosa Dicks., 645
Jungermannia victoriensis (Bibby) E.A.Hodgs., 707
Jungermanniaceae Rchb., **637**
Subfam. Chandonanthoideae Inoue, **640**
Subfam. Eremonotoideae R.M.Schust., 639
Subfam. Gottschelioideae R.M.Schust., 639
Subfam. Jamesonielloideae Inoue, **713**
Subfam. Jungermannioideae Dumort., **694**
Subfam. Lophozioideae Macvicar, **67**, **80**, **83**, **645**
Subfam. Notoscyphoideae R.M.Schust., 639
Subfam. Scaphophyloideae R.M.Schust., 639
Jungermanniales H.Klinggr., **68**
Suborder Antheliineae R.M.Schust., **546**
Suborder Cephaloziineae R.M.Schust., **551**
Suborder Herbertineae R.M.Schust., **107**
Suborder Jungermanniineae R.M.Schust., **637**
Suborder Lepicoleineae R.M.Schust., **93**
Suborder Lepidoziineae R.M.Schust., **194**
Suborder Neogrollineae J.J.Engel & Braggins, **102**
Suborder Trichotemnomatineae J.J.Engel, **542**

Kantia sphagnicola Arnell & J.Perss., 534
Kantius Gray, 533
Krunodiplophyllum Grolle, 746
Kurzia G.Martens, 71, **358**
Subg. Dendrolembidium (Herzog) Grolle, **379**
Subg. *Leucolepidozia* R.M.Schust., 324
Subg. Micrisophylla (Fulford) J.J.Engel *ex* R.M.Schust., 359
Subg. Microlepidozia (Spruce) R.M.Schust., **361**
Subg. *Nanolepidozia* R.M.Schust., 339
Sect. Compactae R.M.Schust., **376**
Sect. Helophilae R.M.Schust., **361**
Sect. *Megalembidium* (R.M.Schust.) Grolle, 525
Sect. Microlepidozia, **364**
Sect. Moniliformes J.J.Engel, **373**
Kurzia allisonii (Herzog) Grolle, 371
Kurzia calcarata (Steph.) Grolle, **364**, **366**
Kurzia capillaris (Sw.) Grolle, 361
Kurzia compacta (Steph.) Grolle, **377**
Kurzia crenacanthoidea G.Martens, 359
Kurzia cucullifolia (Steph.) R.M.Schust., 359
Kurzia dendroides (Carrington & Pearson) Grolle, 359
Kurzia fragilifolia R.M.Schust., 334
Kurzia fragillima (Herzog) Grolle, 359
Kurzia helophila R.M.Schust., **362**
Kurzia helophila var. flaccida R.M.Schust. *ex* J.J.Engel, **364**
Kurzia helophila var. helophila, **363**
Kurzia hippuroides (Hook.f. & Taylor) Grolle, **368**
Kurzia hippuroides var. hippuroides, **371**
Kurzia hippuroides var. ornata J.J.Engel & Merrill, **373**
Kurzia insulana (W.Martin & E.A.Hodgs.) Grolle, 529
Kurzia mollis (Steph.) J.J.Engel & R.M.Schust., 359
Kurzia moniliformis J.J.Engel, **373**
Kurzia pallescens Grolle, 331
Kurzia quadriseta Grolle, 331
Kurzia quadriseta var. *trilobata* R.M.Schust., 333
Kurzia quinquespina J.J.Engel & Merrill, 347
Kurzia saddlensis (Besch. & C.Massal.) Grolle, 359
Kurzia setiformis (De Not.) J.J.Engel & R.M.Schust., 359
Kurzia sexfida (Steph.) Grolle, 359
Kurzia temnomoides R.M.Schust., 366
Kurzia tenax (Grev.) Grolle, **379**
Kurzia trilobata, 359
Kurzia verticillata (Carrington) Grolle, 359
Kymatocalyx Herzog, 567
Kymatocalyx africanus Váňa & Wigginton, 567
Kymatolejeunea Grolle, **93**

Lamellocolea J.J.Engel, **77**
Leiocolea (Müll.Frib.) Buch, 645
Leiomitra Lindb., 73, **173**
Leiomitra breviseta (Steph.) R.M.Schust., 175
Leiomitra elegans (Lehm.) Hässel, 175
Leiomitra julacea Hatcher *ex* J.J.Engel, 170
Leiomitra lanata (Hook.) R.M.Schust., **176**
Leiomitra smaragdina Hässel, 175
Leiomitra tomentosa (Sw.) Lindb., 175
Lejeunea Lib., **92**
Lejeuneaceae Casares-Gil, **91**
Subfam. Ptychanthoideae Mizut., **89**
Subfam. Tuyamaelloideae R.M.Schust. & Kachroo, **91**
Lembidium Mitt., 74, 79, **503**
Subg. *Isodictyon* Herzog, 509
Lembidium anomalum Rodway, 500
Lembidium australe (Steph.) Grolle, 521
Lembidium berggrenii Herzog, 524
Lembidium cucullatum E.A.Hodgs., 503
Lembidium denticulatum Steph., 523
Lembidium insulanum W.Martin & E.A.Hodgs., 529
Lembidium isodictyon Herzog, 517
Lembidium longifolium R.M.Schust., **506**
Lembidium nutans (Hook.f. & Taylor) Mitt., **508**
Lembidium stereophyllum Herzog, 521
Lembidium tenax (Grev.) Steph., 379

INDEX

Leperoma scolopendra (Hook.) Bastow, 99
Lepicolea Dumort., 73, **95**
Lepicolea attenuata (Mitt.) Steph., **95**
Lepicolea magellanica (Gola) Solari, 94
Lepicolea ochroleuca (Spreng.) Spruce, 94
Lepicolea rigida (De Not.) E.B.Scott, 94
Lepicolea scolopendra (Hook.) Dumort. *ex* Trevis., **99**
Lepicoleaceae R.M.Schust., **94**
Lepidogyna R.M.Schust., **91**
Lepidolaena Dumort., **91**
Lepidolaenaceae Nakai, **90**
Lepidozia (Dumort.) Dumort., 71, **195**
Subg. *Apiculo-lepidozia* S.W.Arnell, 381
Subg. *Austrolepidozia* (R.M.Schust.) R.M.Schust., 256
Subg. Chaetolepidozia R.M.Schust., 197
Subg. Cladolepidozia R.M.Schust., 197
Subg. Dendrolepidozia R.M.Schust., **201**
Subg. Glaucolepidozia R.M.Schust., **259**
Subg. *Incisae* Lindenb., 256
Subg. Mastigolepidozia R.M.Schust., **204**
Subg. *Microlepidozia* Spruce, 358, 361
Subg. Notholepidozia R.M.Schust., **206**
Subg. *Telaranea* (Spruce *ex* Schiffn.) Müll.Frib., 270
Sect. Austrolepidozia R.M.Schust., **256**
Sect. *Capillares* Gottsche, 324
Sect. Kirkii R.M.Schust., **248**
Sect. Microphyllae (Lindenb.) Grolle, **204**
Sect. *Neolepidozia* (Fulford & J.Taylor) Piippo, 279
Sect. Notholepidozia, **211**
Sect. Pendulinae R.M.Schust., **206**
Sect. Setigerae R.M.Schust., **209**
Lepidozia acantha J.J.Engel, **239**
Lepidozia albula (Hook.f. & Taylor) Gottsche, 256
Lepidozia allisonii Herzog, 371
Lepidozia angelii Gottsche *ex* Steph., 250
Lepidozia asperifolia Steph., 227
Lepidozia beckettiana Steph., 289
Lepidozia bicuspidata C.Massal., 473
Lepidozia bidens J.J.Engel, **245**
Lepidozia bisbifida Steph., **262**
Lepidozia breviloba Steph., 211
Lepidozia brevipinna Pearson, 262
Lepidozia calcarata Steph., 366
Lepidozia cancellata Colenso, 305
Lepidozia cavernarum Herzog, 468
Lepidozia chaetophylla Spruce, 271
Lepidozia colensoana Steph., 223
Lepidozia compacta Steph., 377
Lepidozia concinna Colenso, **223**
Lepidozia corticola Steph., 300
Lepidozia cupressina var. *pendulina* (Hook.) Lehm. & Lindenb., 206
Lepidozia dentifolia Steph., 248
Lepidozia digitata Herzog, **264**
Lepidozia dispar (Mont. *ex* Taylor & Hook.f.) Mont., 371
Lepidozia elegans Colenso, 309
Lepidozia elobata R.M.Schust., **241**
Lepidozia fugax J.J.Engel, **232**
Lepidozia gibbsiana Steph., 291
Lepidozia gigantea Steph., 206
Lepidozia glaucescens J.J.Engel, **266**
Lepidozia glaucophylla (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, **259**
Lepidozia gottscheana Lindenb., 300
Lepidozia gracillima Carrington & Pearson, 300
Lepidozia grossiseta Steph., 285
Lepidozia hepaticola Steph., 328
Lepidozia herzogii E.A.Hodgs., 350
Lepidozia hippuroides (Hook.f. & Taylor) Steph., 371
Lepidozia hirta Steph., **250**
Lepidozia integristipula Steph., 387
Lepidozia kirkii Steph., **248**
Lepidozia laevifolia (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, **227**
Lepidozia laevifolia var. acutiloba J.J.Engel, **231**
Lepidozia laevifolia var. alpina R.M.Schust. & J.J.Engel, **232**
Lepidozia laevifolia var. laevifolia, **231**
Lepidozia latiloba Colenso, 223
Lepidozia leptodictyon Herzog, 461
Lepidozia leucocarpa Colenso, 328
Lepidozia lindenbergii Gottsche, 324
Lepidozia longifissa Steph., 201
Lepidozia martinii E.A.Hodgs., 339
Lepidozia meridiana E.A.Hodgs., 276
Lepidozia meridiana var. *paludicola* E.A.Hodgs., 307
Lepidozia microphylla (Hook.) Lindenb., **204**
Lepidozia minuta Colenso, 227
Lepidozia minutissima Colenso, 328
Lepidozia mooreana Steph., 316
Lepidozia multipinna Steph., 204
Lepidozia novae-zelandiae Steph., **237**
Lepidozia novae-zelandiae var. heterostipa R.M.Schust., **239**
Lepidozia novae-zelandiae var. minima R.M.Schust., **239**
Lepidozia novae-zelandiae var. novae-zelandiae, **238**
Lepidozia obtusiloba Steph., **213**
Lepidozia obtusiloba var. obtusiloba, **217**
Lepidozia obtusiloba var. parvula J.J.Engel, **219**
Lepidozia occulta Colenso, 328
Lepidozia oldfieldiana Steph., 281
Lepidozia ornata J.J.Engel, **219**
Lepidozia papillata Steph., 227
Lepidozia parvitexta Steph., 213
Lepidozia patentissima (Hook.f. & Taylor) Gottsche, 295
Lepidozia pendulina (Hook.) Lindenb., **206**
Lepidozia praenitens (Lehm. & Lindenb.) Gottsche, 285
Lepidozia procera Mitt., **211**
Lepidozia pulcherrima Steph., 319
Lepidozia pumila J.J.Engel, **242**
Lepidozia radiata Steph., 330
Lepidozia randii S.W.Arnell, 160
Lepidozia remotifolia E.A.Hodgs., 316

Lepidozia retrusa Colenso, 227
Lepidozia roseana Steph., 304
Lepidozia serrulata J.J.Engel, **253**
Lepidozia setigera Steph., **209**
Lepidozia spinosissima (Hook.f. & Taylor) Mitt., **201**
Lepidozia subquadrata Steph., 262
Lepidozia subsimplex Steph., 464
Lepidozia subverticillata Colenso, 328
Lepidozia tenax (Grev.) Lindenb., 379
Lepidozia tetradactyla (Hook.f. & Taylor) Gottsche, 336
Lepidozia tetrapila Hook.f. & Taylor, 301
Lepidozia tridactylis (Lehm. & Lindenb.) Mont., 281
Lepidozia tripilosa Steph., 309
Lepidozia ulothrix (Schwägr.) Lindenb., **256**
Lepidoziaceae Limpr., **76**, **194**
Subfam. Bazzanioideae Rodway, **390**
Subfam. Drucelloideae (Boesen) R.M.Schust., **385**
Subfam. Lembidioideae R.M.Schust., **499**
Subfam. Lepidozioideae Limpr., **195**
Subfam. Megalembidioideae J.J.Engel, **525**
Subfam. Micropterygioideae Grolle, 195
Subfam. *Neogrolleoideae* R.M.Schust., 102
Subfam. Protocephalozioideae R.M.Schust., 195
Subfam. Zoopsidoideae R.M.Schust., **457**
Tribe *Drucellae* Boesen, 385
Lepidoziella varians (Gottsche) Mahu, 600
Lepidoziopsis E.A.Hodgs., 195, 259
Lepidoziopsis glaucophylla (Hook.f. & Taylor) E.A.Hodgs., 259
Leptolejeunea (Spruce) Schiffn., **93**
Leptophyllopsis R.M.Schust., **79**
Leptoscyphus Mitt., **77**, **78**
Lethocolea Mitt., **88**
Leucosarmentum Fulford, 463
Lophochaete R.M.Schust., 141
Lophocoleaceae, **76**, **77**, **80**
Lopholejeunea (Spruce) Schiffn., **90**
Lophonardia R.M.Schust., 784
Lophonardia caespitosa R.M.Schust., 784
Lophozia (Dumort.) Dumort., 81, 84, 85, **645**
Subg. Barbilophozia (Loeske) Müll.Frib., 646
Subg. Hypolophozia R.M.Schust., 646
Subg. Isopaches (Buch) R.M.Schust., **663**
Subg. Lophozia, **662**
Subg. *Massula* Müll.Frib., 645
Subg. Orthocaulis (Buch) R.M.Schust., 646
Subg. Protolophozia R.M.Schust., 646, **648**
Subg. Schistochilopsis N.Kitag., 646
Lophozia androgyna R.M.Schust., 646
Lophozia anomala R.M.Schust., 646
Lophozia argentina (Steph.) R.M.Schust., 646
Lophozia autoica R.M.Schust., **649**
Lophozia autoica var. *subalpina* R.M.Schust., 652
Lophozia badia (Gottsche) Steph., 561
Lophozia bicrenata (Schmid. *ex* Hoffm.) Dumort., **665**
Lophozia crispata R.M.Schust., 646
Lophozia druceae Grolle & E.A.Hodgs., **661**
Lophozia excisa (Dicks.) Dumort., **662**
Lophozia exsecta (Schmid. *ex* Schrad.) Dumort., 667
Lophozia gymnocoleopsis R.M.Schust. & J.J.Engel, 646
Lophozia hatcheri (A.Evans) Steph., 646
Lophozia herzogiana E.A.Hodgs. & Grolle, **648**
Lophozia innominata E.A.Hodgs., 663
Lophozia lancistipa (Grolle) R.M.Schust., 646
Lophozia laxifolia (Mont.) Grolle, 646
Lophozia leucorhiza (Mitt.) R.M.Schust., 646
Lophozia monoica (E.A.Hodgs.) J.J.Engel, **655**
Lophozia multicuspidata (Hook.f. & Taylor) Grolle, **657**
Lophozia nivicola R.M.Schust., **654**
Lophozia patagonica Herzog & Grolle, 646
Lophozia perigonialis (Hook.f. & Taylor) Grolle, 692
Lophozia propagulifera (Gottsche) Steph., 662
Lophozia pumicicola Berggr., **663**
Lophozia subalpina (R.M.Schust.) R.M.Schust., **652**
Lophozia tasmanica R.M.Schust., 646
Lophozia ventricosa (Dicks.) Dumort., 645
Lophoziella Douin & Schiffn., 578

Maculia E.A.Hodgs., 523
Maculia berggrenii (Herzog) E.A.Hodgs., 524
Maculia filosa E.A.Hodgs., 524
Marsupella Dumort., 82, **798**
Subg. Marsupella, **799**
Marsupella boeckii (Austin) Lindb., 799
Marsupella capensis S.W.Arnell, 799
Marsupella emarginata (Ehrh.) Dumort., 799
Marsupella lacerata (Steph.) Váňa, 799
Marsupella lorentziana Steph., 799
Marsupella miniata (Lindenb. & Gottsche) Grolle, 799
Marsupella minutula Hässel, 799
Marsupella sparsifolia (Lindb.) Dumort., **801**
Marsupella sparsifolia subsp. childii R.M.Schust., **801**
Marsupella sparsifolia subsp. sparsifolia, 801
Marsupella sprucei (Limpr.) Bernet, **799**
Marsupella ustulata var. *sprucei* (Limpr.) R.M.Schust., 799
Marsupellaceae Buch, 783
Marsupidium Mitt., **84**, **86**
Marsupidium capillare Berggr., 621
Marsupidium piliferum Steph., 610
Martinellia nemorosa (L.) Lindb., 771
Martinellia vertebralis (Taylor *ex* Gottsche, Lindenb. & Nees) Trevis., 780
Martinellius nemorosus (L.) M.Bernet & Gray, 771
Martinellius undulatus (L.) Gray, 768
Massula Müll.Frib. *ex* Schljakov, 645
Mastigobryum sect. *Connatae* Steph., 423
Mastigobryum sect. *Vittata* Steph., 442
Mastigobryum adnexum (Lehm. & Lindenb.) Mont., 423
Mastigobryum adnexum fo. *exarmatum* Steph., 425
Mastigobryum amoenum Colenso, 398
Mastigobryum anisostomum (Lehm. & Lindenb.) Gottsche, 407

INDEX

Mastigobryum atro-virens (Hook.f. & Taylor) Gottsche, 407
Mastigobryum colensoanum Mitt., 398
Mastigobryum compactum Colenso, 423
Mastigobryum concinnatum Colenso, 431
Mastigobryum convexum (Thunb.) Lindenb., 442
Mastigobryum cunninghamii (Steph.) Steph., 402
Mastigobryum delicatulum Colenso, 449
Mastigobryum elegans Colenso, 418
Mastigobryum erosifolium Steph., 398
Mastigobryum fissistipum Steph., 442
Mastigobryum fugax Colenso, 442
Mastigobryum heterodontum Colenso, 425
Mastigobryum heterophyllum Colenso, 431
Mastigobryum hochstetteri Reicht., 431
Mastigobryum imbricatistipulum Colenso, 431
Mastigobryum involutum (Mont.) Lindenb., 418
Mastigobryum kirkianum Steph., 425
Mastigobryum laceratum (Steph.) Steph., 425
Mastigobryum macro-amphigastrum Colenso, 423
Mastigobryum macrodontum Colenso, 423
Mastigobryum minutulum Colenso, 398
Mastigobryum mittenii Steph., 431
Mastigobryum monilinerve (Lehm. & Lindenb.) Nees, 446
Mastigobryum mooreanum (Steph.) Steph., 409
Mastigobryum nitens Colenso, 424
Mastigobryum novae-hollandiae (Nees) Nees, 423
Mastigobryum novae-hollandiae f. γ 2 *aucklandicum* Lindenb. & Gottsche, 431
M*astigobryum novae-hollandiae* f. τ 3 *submuticum* Lindenb. & Gottsche, 422
Mastigobryum novae-zelandiae Mitt., 436
Mastigobryum nutans (Hook.f. & Taylor) Gottsche, 508
Mastigobryum obscurum Colenso, 449
Mastigobryum obtusatum Colenso, 442
Mastigobryum obtusistipulum Colenso, 449
Mastigobryum olivaceum Colenso, 423
Mastigobryum parasiticum Colenso, 423
Mastigobryum polyodon Colenso, 423
Mastigobryum pusillum Colenso, 431
Mastigobryum quadratum Colenso, 431
Mastigobryum reflexistipulum Lindenb. & Gottsche, 418
Mastigobryum semicordatum Lindenb. & Gottsche, 423
Mastigobryum similis Colenso, 431
Mastigobryum smaragdinum Colenso, 398
Mastigobryum spectabile Steph., 436
Mastigobryum taylorianum Mitt., 449
Mastigobryum verticale (Steph.) Steph., 395
Mastigobryum vulcanicum Colenso, 425
Mastigolejeunea, **89**
Mastigopelma Mitt., 195
Mastigophora sect. *Schisma* Nees, 108
Mastigophora albula (Hook.f. & Taylor) Trevis., 256
Mastigophora beckettiana Steph., 137
Mastigophora dispar (Mont. *ex* Taylor & Hook.f.) Trevis., 371
Mastigophora glaucophylla (Hook.f. & Taylor) Trevis., 259
Mastigophora gottscheana (Lindenb.) Trevis., 300
Mastigophora laevifolia (Hook.f. & Taylor) Trevis., 227
Mastigophora lindenbergii (Gottsche) Trevis., 324
Mastigophora microphylla (Hook.) Mont., 204
Mastigophora patentissima (Hook.f. & Taylor) Trevis., 295
Mastigophora pendulina (Hook.) Trevis., 206
Mastigophora praenitens (Lehm. & Lindenb.) Trevis., 285
Mastigophora subtrifida (Hook.f. & Taylor) E.A.Hodgs., 120
Mastigophora tenax (Grev.) Trevis., 379
Mastigophora tetradactyla (Hook.f. & Taylor) Trevis., 336
Mastigophora tetrapila (Hook.f. & Taylor) Trevis., 301
Mastigophora ulothrix (Schwägr.) Trevis., 256
Megalembidium R.M.Schust., 71, **525**
Megalembidium insulanum (W.Martin & E.A.Hodgs.) R.M.Schust., **529**
Mesophylla tasmanica (Hook.f. & Taylor) Trevis., 719
Metacalypogeia (S.Hatt.) Inoue, 533
Metacalypogeia cordifolia (Steph.) Inoue, 533
Metacalypogeia montana (Horik.) Inoue, 533
Metahygrobiella R.M.Schust., 83, 85, **553**
Metahygrobiella acuminata (Herzog) R.M.Schust., 553
Metahygrobiella albula (Steph.) Grolle, 555
Metahygrobiella australis (Steph.) R.M.Schust., 521
Metahygrobiella chilensis J.J.Engel & R.M.Schust., 560
Metahygrobiella cylindrica E.A.Hodgs. & Herzog, 555
Metahygrobiella drucei R.M.Schust., **555**
Metahygrobiella lucens (A.Evans) H.A.Mill., 555
Metahygrobiella monoica E.A.Hodgs., 655
Metahygrobiella tayloriae E.A.Hodgs., 555
Metahygrobiella tubulata (Hook.f. & Taylor) R.M.Schust. *ex* J.J.Engel, 555
Micrisophylla Fulford, 358
Micrisophylla leptodictyon (Herzog) E.A.Hodgs., 461
Microlepidozia (Spruce) Jörg., 358
Microlepidozia allisonii (Herzog) R.M.Schust., 371
Microlepidozia calcarata (Steph.) R.M.Schust., 366
Microlepidozia capillaris (Sw.) Fulford, 361
Microlepidozia compacta (Steph.) R.M.Schust., 377
Microlepidozia hippuroides (Hook.f. & Taylor) E.A.Hodgs., 371
Microlepidozia quadriseta (Grolle) R.M.Schust., 331
Microlepidozia quadriseta fo. *pallescens* (Grolle) R.M.Schust., 331
Micropterygium Lindenb., Nees & Gottsche, 195
Micropterygium nutans (Hook.f. & Taylor) Mitt., 508
Mnioloma Herzog, 74, **537**
Mnioloma fuscum (Lehm.) R.M.Schust., 539
Mnioloma novaezelandiae J.J.Engel, **539**
Mnioloma rhynchophyllum Herzog, 539
Mniopsis Dumort., 60
Mnium fissum L., 534

Monodactylopsis (R.M.Schust.) R.M.Schust., 195
Mytilopsis Spruce, 195

Nanomarsupella R.M.Schust., 784
Nardia Gray, 639
Nardia inundata (Hook.f. & Taylor) Steph., 707
Nardia patellata Berggr., 707
Nardia perigonialis (Hook.f. & Taylor) Trevis., 692
Nardia sparsifolia (Lindb.) Lindb., 801
Neogrollea E.A.Hodgs., 70, 75, **102**
Neogrollea notabilis E.A.Hodgs., **105**
Neogrolleaceae (R.M.Schust.) J.J.Engel & Braggins, **70**, **102**
Neolepidozia Fulford & J.Taylor, 270, 279
Neolepidozia corticola (Steph.) Fulford & J.Taylor, 300
Neolepidozia gottscheana (Lindenb.) Fulford & J.Taylor, 300
Neolepidozia roseana (Steph.) Fulford & J.Taylor, 304
Neolepidozia tetradactyla (Hook.f. & Taylor) Fulford & J.Taylor, 336
Nephelolejeunea Grolle, **91**
Nothogymnomitrion R.M.Schust., 83, 784, **795**
Nothogymnomitrion erosum (Carrington & Pearson) R.M.Schust., **797**
Nothostrepta R.M.Schust., 84, 85, 639
Nothostrepta bifida (Steph.) R.M.Schust., 639
Nothostrepta longissima (Steph.) R.M.Schust., 639
Notoscyphus Mitt., 639
Notoscyphus belangerianus (Lehm. & Lindenb.) Mitt., 639
Nowellia Mitt., 552

Obtusifolium S.W.Arnell, 645
Odontoschisma (Dumort.) Dumort., 552
Odontoschisma falcata (Hook.) Trevis., 621
Odontoschisma occlusum (Hook.f. & Taylor) Trevis., 625
Odontoseries Fulford, 195
Olgantha R.M.Schust., 108
Olgantha eophylla R.M.Schust., 108
Orthocaulis longiflorus Herzog, 646

Pachyglossa Herzog & Grolle, **76**
Pachyschistochila R.M.Schust. & J.J.Engel, **90**
Paracromastigaceae Fulford, 194
Paracromastigum Fulford & J.Taylor, 70, 79, **463**
Paracromastigum ceratophyllum (Spruce) R.M.Schust., 484
Paracromastigum drucei (R.M.Schust.) R.M.Schust., **465**
Paracromastigum dusenii (Steph.) R.M.Schust., 464
Paracromastigum fiordlandiae R.M.Schust. & J.J.Engel, **466**
Paracromastigum fissifolium (Steph.) R.M.Schust., 484
Paracromastigum furcifolium (Steph.) R.M.Schust., **468**
Paracromastigum kirkii (Steph.) R.M.Schust., 471
Paracromastigum longiscyphum (Taylor) R.M.Schust. & J.J.Engel, 464
Paracromastigum macrostipum (Steph.) R.M.Schust., **471**
Paracromastigum stipulatum (Herzog) Fulford, 464
Paracromastigum subsimplex (Steph.) Fulford & J.Taylor, 464
Paracromastigum succulentum (Sim) J.J.Engel & Merrill, 464
Paracromastigum tristanianum (R.M.Schust.) J.J.Engel & R.M.Schust., 464
Paramomitrion R.M.Schust., 639, 785
Paraschistochila R.M.Schust., **88**
Parentia Léman, 533
Pedinophyllopsis R.M.Schust. & Inoue, 77
Pedinophyllum (Lindb.) Lindb., **87**
Perssoniella Herzog, 88
Phragmatocolea Grolle, 639
Phycolepidozia R.M.Schust., 194
Phycolepidoziaceae R.M.Schust., 194
Pigafettoa C.Massal., 75, 77
Pisanoa Hässel, 639
Plagiochila (Dumort.) Dumort., **81**, **84**, **85**, **87**
Plagiochila appressifolia Steph., 621
Plagiochila capillaris (Berggr.) E.A.Hodgs., 621
Plagiochila clandestina Mont., 775
Plagiochila falcata (Hook.) Gottsche, 621
Plagiochila inaequalis Steph., 621
Plagiochila inversa Sande Lac., 629
Plagiochila intermixta Colenso, 621
Plagiochila nemorosa (L.) Mont. & Nees, 771
Plagiochila pusilla Mont., 621
Plagiochila subpetiolata Colenso, 621
Plagiochila subsimilis Colenso, 8
Plagiochila undulata (L.) Mont. & Nees, 768
Plagiochilaceae Buch, **80**, 639
Subfam. Syzygielloideae R.M.Schust., 639
Plagiochilion S.Hatt., **81**
Plectocolea cambewarrana (Steph.) Herzog, 703
Pleurocladopsis R.M.Schust., 74
Pleurocladula Grolle, 552
Pleuroschisma sect. *Lepidozia* Dumort., 195
Plicanthus R.M.Schust., 638
Poeltia Grolle, 785
Porella L., **89**
Prasanthus Lindb. & Arnell, 784
Prasanthus suecicus (Gottsche) Lindenb. & Arnell, 784
Prionolobus (Spruce) Schiffn., 578
Protocephalozia (Spruce) Goebel, 195
Protocephaloziella Douin, 578
Protolophozia (R.M.Schust.) Schljakov, 645
Protomarsupella R.M.Schust., 570, 572
Protomarsupella scottii R.M.Schust., 572
Protosyzygiella (Inoue) R.M.Schust., 81, 639
Protosyzygiella pseudoconnexa (Herzog) R.M.Schust., 639
Pseudocephalozia R.M.Schust., 71, **457**
Subg. Lobulatae (R.M.Schust.) R.M.Schust., 457
Pseudocephalozia cucullata J.J.Engel & R.M.Schust., 458

INDEX

Pseudocephalozia drucei R.M.Schust., 465
Pseudocephalozia lepidozioides R.M.Schust., **461**
Pseudocephalozia leptodictyon R.M.Schust., 462
Pseudocephalozia lobulata (Herzog) R.M.Schust., 458
Pseudocephalozia macrostipa (Steph.) R.M.Schust., 471
Pseudocephalozia paludicola R.M.Schust., **459**
Pseudocephalozia quadriloba (Steph.) R.M.Schust., 458
Pseudocephaloziella R.M.Schust., 638
Pseudolepicolea Fulford & J.Taylor, 71, 140
Pseudolepicolea quadrilaciniata (Sullivan) Fulford & J.Taylor, 141
Pseudolepicoleaceae Fulford & J.Taylor, **140**
  Subfam. Blepharostomatoideae Grolle, 141
  Subfam. Chaetocoleoideae R.M.Schust., 141
  Subfam. Temnomoideae R.M.Schust., **141**
  Subfam. *Trichocoleoideae* Nakai, 141
Pseudolophocolea R.M.Schust., **81**
Pseudomarsupidium Herzog, 86, **609**
Pseudomarsupidium areocinctum (R.M.Schust.) J.J.Engel, 610
Pseudomarsupidium crossii (Spruce) J.J.Engel, 610
Pseudomarsupidium decipiens (Hook.) Grolle, 609
Pseudomarsupidium piliferum (Steph.) Herzog *ex* Grolle, **610**
Psiloclada Mitt., 71, **381**
Psiloclada clandestina Mitt., **382**
Psiloclada clandestina subsp. clandestina, **382**
Psiloclada clandestina subsp. *clandestina* fo. *major* R.M.Schust., 382
Psiloclada clandestina subsp. melanesica R.M.Schust., 382
Psiloclada clandestina subsp. spinosa (S.W.Arnell) R.M.Schust., 382
Psiloclada digitata Colenso, 305
Psiloclada major (R.M.Schust.) J.J.Engel, 382
Psiloclada unguiligera Schiffn., 382
Pteropsiella Spruce, 195
Ptilidium Nees, **73**
Ptychanthus Nees, **90**

Radula Dumort., **89**
Radula nemorosa (L.) Dumort., 771
Radula undulata (L.) Dumort., 768
Rectolejeunea A.Evans, **92**
Regredicaulaceae Fulford, 194
Rhodoplagiochila R.M.Schust., 640
Rhodoplagiochila rosea R.M.Schust., 640
Rhopalanthus Lindb., 60
Roivainenia Perss., 84, 638
Roivainenia tasmanica (Rodway) Grolle, 641

Saccogynidium Grolle, **77**
Sarcoscyphus perigonialis (Hook.f. & Taylor) Gottsche, 692
Sarcoscyphus sparsifolius Lindb., 801
Sarcoscyphus sprucei Limpr., 799
Scalia Spruce, 60
Scalius Gray, 60
Scapania (Dumort.) Dumort., 89, **765**
  Subg. Jensenia S.W.Arnell, 767
  Subg. Macroscapania R.M.Schust., 767
  Subg. Scapania, **767**
  Subg. Scapaniella (Buch) Jörg., 767
  Sect. Nemorosae (Müll.Frib.) Buch, **769**
  Sect. Scapania, **768**
  Sect. *Undulatae* Buch, 768
Scapania cuspiduligera (Nees) Müll.Frib., 767
Scapania esterhuyseniae S.W.Arnell, 767
Scapania exsecta (Schmid. *ex* Schrad.) Aust., 667
Scapania gamundiae R.M.Schust., 767
Scapania hedbergii S.W.Arnell, 767
Scapania macgregorii Steph., 767
Scapania nemorosa (L.) Dumort., **771**
Scapania obcordata (Berggr.) S.W.Arnell, 767
Scapania portoricensis Gottsche, 767
Scapania undulata (L.) Dumort., **768**
Scapania valdonsmithii R.M.Schust., 767
Scapania vertebralis Taylor *ex* Gottsche, 780
Scapaniaceae Mig., **744**
  Subfam. *Blepharidophylloideae* R.M.Schust., 773
  Subfam. Delavayelloideae Grolle, 745
Scaphophyllum Inoue, 639
Schiffneria Steph., 552
Schisma Dumort., 108
Schisma alpinum Steph., 109
Schisma oldfieldianum Steph., 109
Schistochila Dumort., **90**
Schistochilaceae Dumort., **90**
Schofieldia J.D.Godfrey, 552
Sendtnera Endl., 108
Sendtnera attenuata Mitt., 95
Sendtnera quadrifida Colenso, 95
Sendtnera scolopendra (Hook.) Nees, 99
Sendtnera spinosissima Hook.f. & Taylor, 201
Siphonolejeunea Herzog, **91**
Solenostoma Mitt., 87, **694**
  Subg. Plectocolea Mitt., 695
  Subg. Solenostoma, **695**
Solenostoma brevissima Pearson, 707
Solenostoma callithrix (Lindenb. & Gottsche) Steph., 695
Solenostoma contexta Kaal. *ex* Steph., 703
Solenostoma crassulum (Nees & Mont.) Steph., 695
Solenostoma cryptogynum R.M.Schust. *ex* J.J.Engel, **705**
Solenostoma decolor (Schiffn.) R.M.Schust., 697
Solenostoma hodgsoniae (Grolle) J.J.Engel, **699**
Solenostoma inundatum (Hook.f. & Taylor) Mitt. *ex* Steph., **707**
Solenostoma novaezelandiae R.M.Schust., 713
Solenostoma orbiculatum (Colenso) R.M.Schust., **703**
Solenostoma patellata (Berggr.) Steph., 707
Solenostoma rufiflorum (Colenso) J.J.Engel, **709**
Solenostoma tersum (Nees) Mitt., 695

Solenostoma totipapillosum (E.A.Hodgs.) R.M.Schust., **711**
Sphenolobopsis R.M.Schust. & N.Kitag., 638
Sphenolobopsis kitagawae R.M.Schust., 638
Sphenolobopsis pearsonii (Spruce) R.M.Schust. & N.Kitag., 638
Sphenolobus (Lindb.) Berggr., 638
Subg. *Tritomaria* (Schiffn.) Müll.Frib., 666
Sphenolobus exsectus (Schmid. *ex* Schrad.) Steph., 669
Sphenolobus minutus (Schreb. *ex* Cranz) Steph., 674
Sphenolobus nigrus Rodway, 574
Sphenolobus perigonialis (Hook.f. & Taylor) Berggr., 692
Sprucella Steph., 195
Steereomitrium E.O.Campb., 60
Steereomitrium minutum E.O.Campb., 65
Stenolejeunea R.M.Schust., **92**
Stenorrhipis Herzog, 567
Stephaniella Jack, 784
Stephaniellaceae (R.M.Schust.) R.M.Schust., 784
Stephaniellidium S.Winkler *ex* Grolle, 784
Stolonivector J.J.Engel, **80**
Symphyomitra grandifolia (Berggr.) Steph., 699
Syzygiella Spruce, 81, 639

Teinnoma Mitt., 147
Telaranea Spruce *ex* Schiffn., 69, 70, 71, **270**
Subg. Acrolepidozia (R.M.Schust.) R.M.Schust., **276**
Subg. *Neolepidozia* (Fulford & J.Taylor) R.M.Schust., 279
Subg. Telaranea, **279**
Subg. *Tricholepidozia* R.M.Schust., 316
Sect. Cancellatae J.J.Engel & Merrill, **285**
Sect. *Capillares* J.J.Engel & Merrill, 285
Sect. Ceraceae J.J.Engel & Merrill, **309**
Sect. *Glaucolepidozia* R.M.Schust., 309
Sect. *Latifoliae* J.J.Engel & Merrill, 276
Sect. *Neolepidozia* (Fulford & J.Taylor) J.J.Engel & Merrill, 279
Sect. Telaranea, **339**
Sect. Tenuifoliae (R.M.Schust.) J.J.Engel & Merrill, **350**
Sect. Transversae J.J.Engel & Merrill, **324**
Sect. Tricholepidozia (R.M.Schust.) J.J.Engel & Merrill, **316**
Telaranea corticola (Steph.) E.A.Hodgs., 300
Telaranea dispar (Mont. *ex* Taylor & Hook.f.) E.A.Hodgs., 371
Telaranea elegans (Colenso) J.J.Engel & Merrill, **309**
Telaranea exigua R.M.Schust., 350
Telaranea fragilifolia (R.M.Schust.) J.J.Engel & Merrill, **334**
Telaranea gibbsiana (Steph.) E.A.Hodgs., **291**
Telaranea gottscheana (Lindenb.) E.A.Hodgs., 300
Telaranea granulata J.J.Engel & Merrill, **344**
Telaranea grossiseta (Steph.) J.J.Engel & R.M.Schust., 285
Telaranea herzogii (E.A.Hodgs.) E.A.Hodgs., **350**
Telaranea hodgsoniae J.J.Engel & Merrill, **293**
Telaranea inaequalis R.M.Schust. *ex* J.J.Engel & Merrill, **357**
Telaranea lindenbergii (Gottsche) J.J.Engel & Merrill, **324**
Telaranea lindenbergii var. complanata J.J.Engel & Merrill, **327**
Telaranea lindenbergii var. lindenbergii, **328**
Telaranea lindenbergii var. mellea J.J.Engel & Merrill, **330**
Telaranea lindenbergii var. papillata J.J.Engel & Merrill, **328**
Telaranea longii Paton, 336
Telaranea martinii (E.A.Hodgs.) R.M.Schust., **339**
Telaranea meridiana (E.A.Hodgs.) E.A.Hodgs., **276**
Telaranea nivicola R.M.Schust., **343**
Telaranea pallescens (Grolle) J.J.Engel & Merrill, **331**
Telaranea paludicola (E.A.Hodgs.) E.A.Hodgs., **307**
Telaranea patentissima (Hook.f. & Taylor) E.A.Hodgs., **295**
Telaranea patentissima var. ampliata J.J.Engel & Merrill, **300**
Telaranea patentissima var. patentissima, **300**
Telaranea patentissima var. zebrina J.J.Engel & Merrill, **300**
Telaranea pennata J.J.Engel & Merrill, **279**
Telaranea perfragilis J.J.Engel & Merrill, **315**
Telaranea praenitens (Lehm. & Lindenb.) E.A.Hodgs., **285**
Telaranea praenitens var. dentifolia J.J.Engel & Merrill, **289**
Telaranea praenitens var. praenitens, **289**
Telaranea pulcherrima (Steph.) R.M.Schust., **319**
Telaranea pulcherrima var. mooreana (Steph.) J.J.Engel & Merrill, 323
Telaranea pulcherrima var. pulcherrima, **323**
Telaranea quinquespina (J.J.Engel & Merrill) J.J.Engel & Merrill, **347**
Telaranea radiata (Steph.) R.M.Schust., 330
Telaranea remotifolia E.A.Hodgs., **316**
Telaranea roseana (Steph.) E.A.Hodgs., 304
Telaranea tetradactyla (Hook.f. & Taylor) E.A.Hodgs., **336**
Telaranea tetrapila (Hook.f. & Taylor) J.J.Engel & Merrill, **301**
Telaranea tetrapila var. cancellata (Colenso) J.J.Engel & Merrill, **305**
Telaranea tetrapila var. roseana (Steph.) J.J.Engel & Merrill, **304**
Telaranea tetrapila var. tetrapila, **307**
Telaranea tridactylis (Lehm. & Lindenb.) J.J.Engel & Merrill, **281**
Telaranea trilobata (R.M.Schust.) J.J.Engel & Merrill, **333**
Telaranea tuberifera J.J.Engel & R.M.Schust., **312**
Temnoma Mitt., 72, 73, **147**
Temnoma angustifolium R.M.Schust., **155**

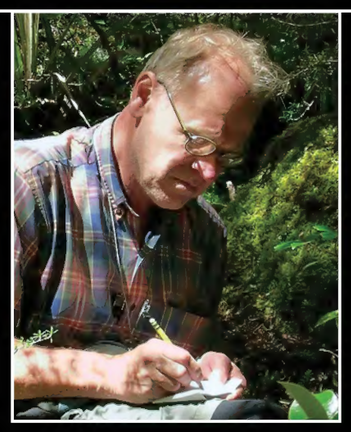
Temnoma chaetophyllum R.M.Schust., 147
Temnoma corrugatum (Steph.) R.M.Schust., 543
Temnoma palmatilobum (E.A.Hodgs.) E.A.Hodgs. & Allison, 156
Temnoma palmatum (Lindb. *ex* Pearson) R.M.Schust., **161**
Temnoma palmatum var. cuneatum R.M.Schust., **164**
Temnoma palmatum var. laxifolium R.M.Schust., **164**
Temnoma palmatum var. palmatum, **163**
Temnoma palmatum var. pseudospiniferum R.M.Schust., **163**
Temnoma paucisetigerum R.M.Schust., **154**
Temnoma pilosum (A.Evans) R.M.Schust., 148
Temnoma pulchellum (Hook.) Mitt., **151**
Temnoma quadrifidum (Mitt.) Mitt., **156**
Temnoma quadripartitum (Hook.) Mitt., **158**
Temnoma quadripartitum var. pseudopungens R.M.Schust., **160**
Temnoma quadripartitum var. quadripartitum, **159**
Temnoma quadripartitum var. randii (S.W.Arnell) R.M.Schust., **160**
Temnoma schusteri E.A.Hodgs. & Allison, 166
Temnoma setigerum (Lindenb.) R.M.Schust., 147
Temnoma subintegrum Fulford, 148
Tetralophozia (R.M.Schust.) Schljakov, 638
Trabacellula Fulford, 552
Triandrophyllum Fulford & Hatcher, 72, **115**
Triandrophyllum fernandeziense (S.W.Arnell) Fulford & Hatcher, 117
Triandrophyllum georgiense (Steph.) Fulford & Hatcher, 117
Triandrophyllum heterophyllum (Steph.) Grolle, 117
Triandrophyllum multicuspidatum (Hook.f. & Taylor) E.A.Hodgs., 657
Triandrophyllum subtrifidum (Hook.f. & Taylor) Fulford & Hatcher, **120**
Triandrophyllum symmetricum J.J.Engel, **119**
Trichocolea Dumort., 73, **179**
  Subg. *Leiomitra* (Lindb.) Spruce, 173
  Sect. *Cryptocaulia* Hatcher *ex* R.M.Schust., 173
Trichocolea australis Steph., 185
Trichocolea elegans Lehm., 183
Trichocolea fragillima Herzog, 180
Trichocolea gracillima Austin, 180
Trichocolea hatcheri E.A.Hodgs., **188**
Trichocolea julacea Hatcher, 170
Trichocolea lanata (Hook.) Nees, 176
Trichocolea mollissima (Hook.f. & Taylor) Gottsche, **183**
Trichocolea novaezelandiae R.M.Schust., 188
Trichocolea pluma (Reinw., Blume & Nees) Mont., 180
Trichocolea polyacantha (Hook.f. & Taylor) Gottsche, 193
Trichocolea rigida R.M.Schust., **180**
Trichocolea tomentella (Ehrh.) Dumort., 180
Trichocoleaceae Nakai, **167**
Trichotemnoma R.M.Schust., 71, **543**
Trichotemnoma corrugatum (Steph.) R.M.Schust., **543**
Trichotemnomaceae R.M.Schust., **542**
Tritomaria Schiffn. *ex* Loeske, 81, **666**
Tritomaria exsecta (Schrad.) Loeske, **667**
Tritomaria exsecta subsp. exsecta J.J.Engel, 669
Tritomaria exsecta subsp. novaezelandiae J.J.Engel, **669**
Tylimanthus Mitt., **84**, **88**
Tylimanthus bisetulus Steph., 610

Vanaea (Inoue & Gradst.) Inoue & Gradst., 639
Vetaforma Fulford & J.Taylor, 71
Vetaforma dusenii (Steph.) Fulford & J.Taylor, 93
Vetaformaceae Fulford & J.Taylor, 93

Wettsteinia Schiffn., 86, **628**
Wettsteinia densiretis (Herzog) Grolle, 629
Wettsteinia inversa (Sande Lac.) Schiffn., 629
Wettsteinia rotundifolia (Horik.) Grolle, 629
Wettsteinia schusteriana Grolle, **629**

Xenocephalozia R.M.Schust., 74, 78

Zoopsidaceae Nakai, 194
Zoopsidella R.M.Schust., 76, **495**
  Subg. Hyalolepidoziopsis R.M.Schust., **496**
  Subg. Hypozoopsis R.M.Schust., 496
  Subg. Zoopsidella, 496
Zoopsidella caledonica (Steph.) R.M.Schust., **496**
Zoopsidella ceratophylla (Spruce) R.M.Schust., 484
Zoopsidella cynosurandra (Spruce *ex* Steph.) R.M.Schust., 496
Zoopsis Hook.f. *ex* Gottsche, Lindenb. & Nees, 69, 76, **477**
  Subg. Amphizoopsis R.M.Schust., **478**
  Subg. Eozoopsis R.M.Schust., **478**
  Subg. Zoopsis, **478**
Zoopsis argentea (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, **488**
Zoopsis argentea var. argentea, **489**
Zoopsis argentea var. flagelliformis (Colenso) R.M.Schust., **490**
Zoopsis basilaris Colenso, 490
Zoopsis bicruris Glenny & E.A.Brown, **491**
Zoopsis caledonica Steph., 496
Zoopsis ceratophylla (Spruce) Hamlin, **484**
Zoopsis cynosurandra Spruce *ex* Steph., 496
Zoopsis flagelliformis Colenso, 490
Zoopsis foliosa Herzog & E.A.Hodgs., 496
Zoopsis leitgebiana (Carrington & Pearson) Bastow, **481**
Zoopsis liukiuensis Horik., 478
Zoopsis macrophylla R.M.Schust., **480**
Zoopsis matawaia M.A.M.Renner, **485**
Zoopsis muscosa Colenso, 490
Zoopsis nitida Glenny, Braggins & R.M.Schust., **492**
Zoopsis setigera K.I.Goebel, 478
Zoopsis setulosa Leitg., **494**
Zoopsis tenuicaulis Colenso, 482



John Engel (left) is curator of bryophytes at the Field Museum, Chicago. He has worked mainly on New Zealand liverworts since 1980, publishing many revisions of New Zealand liverwort families and genera such as *Schistochilaceae*, *Clasmatocolea*, *Lepidozia*, *Telaranea*, and *Balantiopsis* since then. He also has worked on the austral South American liverwort flora, publishing floras of the Falkland Islands/Islas Malvinas and Brunswick Peninsula.

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Line illustration: *Pseudomarsupidium piliferum*. Color images: top, right to left: *Lepicolea scolopendra, Zoopsis setulosa, Diplophyllum verrucosum, Bazzania involuta, Zoopsis argentea*. Bottom, from bottom of page: *Clandarium xiphophyllum, Zoopsis leitgebiana, Solenostoma hodgsoniae*.

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